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**Population regulation, natural enemies,
and host-seeking patterns of
deer ticks, *Ixodes scapularis*
(Acari: Ixodidae)
Final Report**

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Howard S. Ginsberg
and
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**Population regulation, natural enemies, and host-seeking patterns
of deer ticks, *Ixodes Scapularis* (Acari: Ixodidae)**

Final Report

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January, 1996

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Executive Summary

Populations of deer ticks, *Ixodes scapularis*, fluctuated sharply from year to year from 1984 to 1995 at Talisman, Fire Island National Seashore, New York. Tick populations did not vary directly with populations of white-tailed deer, and preliminary indirect evidence suggests density-independent fluctuations. However, small sample size, and variation of tick activity related to ambient temperature and phenology, compromise the reliability of this interpretation. Prevalence of Lyme disease spirochetes, *Borrelia burgdorferi*, in nymphal *I. scapularis* varied from 15.1% in 1993 to 32.1% in 1986.

Leaf-litter dwelling arthropods on Fire Island were collected using Berlese funnels and placed in chambers with immature *I. scapularis*. None of the arthropods tested were voracious-enough predators to serve as biological control agents for *I. scapularis*. Two species of entomopathogenic fungi, *Beauveria bassiana*, and *Verticillium lecanii*, were isolated from *I. scapularis* collected on Fire Island. These fungi killed *I. scapularis* in laboratory pathogenicity tests.

An olfactometer apparatus was developed and tested for use in studies of host-seeking behavior of *I. scapularis*. This apparatus is also useful for bioassays of tick response to pheromones and potential repellents.

Introduction

The deer tick, *Ixodes scapularis* Say (formerly *I. dammini* Spielman, Clifford, Piesman & Corwin; see Oliver et al. 1993) is the primary vector of Lyme disease, or Lyme borreliosis, in the United States. This vector species and the Lyme disease spirochete, *Borrelia burgdorferi* Johnson, Schmid, Hyde, Steigerwalt & Brenner, are endemic to several national park sites in the eastern U.S., especially Fire Island National Seashore (Ginsberg 1992). A great deal of research in the past two decades has focused on the ecology and management of these species (Spielman et al. 1985, Lane et al. 1991, Ginsberg 1993).

Knowledge of the natural population regulatory mechanisms of *I. scapularis* is needed to design efficient management programs for this species. Unfortunately, the factors that regulate *I. scapularis* populations in nature remain controversial. Chapter 1 of this report provides data on population trends of *I. scapularis* on Fire Island from 1987-1995, and provides a preliminary analysis of population regulatory factors for this species. Infection rates with *B. burgdorferi* are also reported. Chapter 2 deals with natural enemies of *I. scapularis*, including arthropod predators, and pathogenic fungi and nematodes. Some of these species show potential for development into biological control agents for *I. scapularis*. Finally, Chapter 3 describes an apparatus that was developed to study host-seeking behavior of *I. scapularis* in the laboratory. This apparatus can be used to study the orientation cues used by questing *I. scapularis* to find hosts, which can suggest ways to interrupt host seeking and thus improve tick-avoidance techniques for humans. The olfactometer device can also be used for bioassays to screen potential tick repellents.

Chapter 1. Population trends of *Ixodes scapularis* at Fire Island National Seashore.

Initial studies of the habitat distribution of *Ixodes scapularis* on Fire Island (FI), and infection rates with Lyme disease spirochetes, *Borrelia burgdorferi*, were performed in 1986 (Ginsberg & Ewing 1989a, Ginsberg 1992). Since 1986, surveillance samples have been taken yearly at Talisman, FI, to track fluctuations in tick population levels and spirochete prevalence in questing nymphs, the stage that transmits most human cases of Lyme disease (Spielman et al. 1985, Fish 1993). The results of this surveillance program are presented in this chapter.

Methods

Ticks were sampled by the flag/drag technique used by Ginsberg & Ewing (1989a,b). Samples were taken in the woods adjacent to Talisman, and east of Talisman between Talisman and Fire Island Pines, during the period of nymphal activity (May through July) each year. Numerous five-minute samples were taken (from 10 to 26 samples each year, mean=15.75) with a small flag (30 x 116 cm) and large drag (76 x 112 cm) made of unbleached cotton muslin. The flag was used to stir up the leaf litter and the drag was pulled behind. Nymphs were collected in 1-dram screw-top vials with moist paper wicks, and were returned to the lab and refrigerated.

Spirochetal infection was determined by dark field microscopy in 1986-1989 (selected slides were confirmed by an indirect immunofluorescent assay using a monoclonal antibody to *B. burgdorferi*; see Ginsberg & Ewing 1989a), and by direct immunofluorescent assay (DFA) in 1991-1995 (using a commercially-available fluorescein-tagged polyclonal antibody to *B. burgdorferi*; Kirkegaard and Perry Laboratories, Gaithersburg, MD, USA; see Carroll et al. 1992).

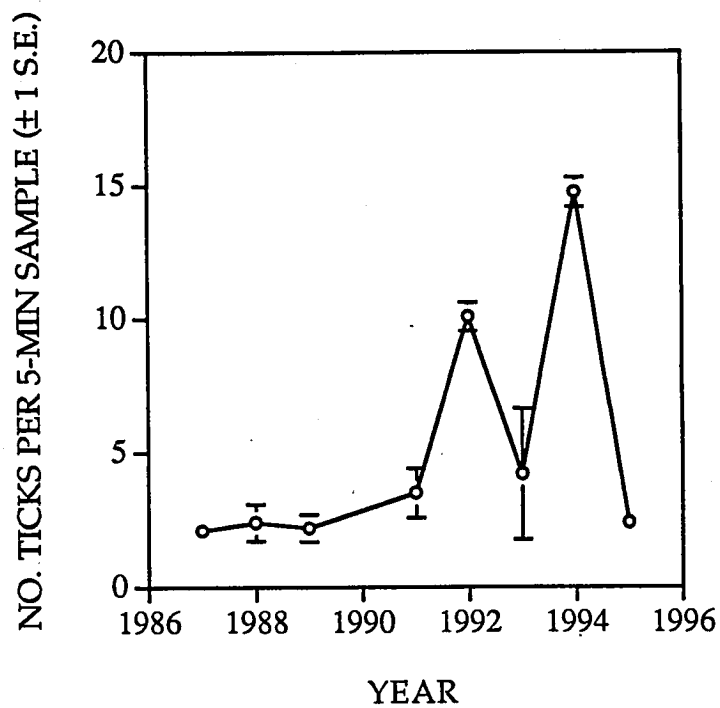
Results and Discussion

Population densities of *I. scapularis* at Talisman (± 1 standard error) are shown in Fig. 1. Note the relative stability in the 1980's followed by broad fluctuations in the 1990's.

Population regulatory mechanisms for *I. scapularis* were reviewed by Fish (1993). Density-independent factors, such as weather, and density-dependent factors, such as host abundance, can potentially regulate populations of *I. scapularis* in nature. The effects of climatic factors have been explored at the northern edge of this species' range in Canada (Lindsay et al. 1995), and relationships with hosts, especially white-tailed deer, have received a great deal of attention in the literature (Spielman 1988, Spielman et al. 1993, Telford 1993).

Wilson et al. (1985) reported a correlation between tick abundance and deer abundance on islands off the coast of Massachusetts. Deer-removal

Figure 1. POPULATION TRENDS, NYMPHAL *Ixodes scapularis*
AT TALISMAN, FIRE ISLAND NATIONAL SEASHORE



experiments were conducted by Wilson et al. (1984, 1988). Lowering deer abundance in these experiments did not lower tick numbers, while elimination of deer resulted in declines in tick populations. These results suggest that deer do not limit tick numbers until populations decline to very low levels. Incremental lowering of deer population size (Deblinger et al. 1993) resulted in broad fluctuations of tick populations around lower mean values than before reduction, but within the range of pre-reduction population sizes.

At Talisman on Fire Island, deer numbers have been increasing since measurement began in 1983. Data from helicopter counts (Fig. 2, data from O'Connell & Sayre 1989, and H.B. Underwood pers comm.) show steady increases in deer populations. This trend differs markedly from trends in tick populations (Fig. 1). Therefore, deer populations on Fire Island apparently do not, by themselves, regulate populations of *I. scapularis*.

One means of assessing the importance of density-dependent vs. density-independent factors in regulating tick populations is to use Morris's key-factor analysis (Southwood 1966). Log population size is plotted against log population size of the previous generation (Fig. 3). The log transformations provide a linear relationship. If population regulation is density-independent, the slope should be one. If density-dependent factors are important the slope should differ from one, because high population levels would result in density-dependent suppression of the subsequent generation. The data for *I. scapularis* at Talisman gave a straight line with a slope of 1.024, suggesting that density-independent factors predominate. The fact that population fluctuations at Talisman closely match fluctuations on Prudence Island, RI (Ginsberg & Hu 1994) suggest that geographically broad-scale factors, such as weather, regulate tick populations. Unfortunately, these relationships are based on only a few data points and are therefore tentative. Indeed, a similar analysis of the Prudence Island data alone produces a negative slope, suggesting that these apparent relationships are artifacts of small sample size (Ginsberg & Hu 1994).

Another problem with reasoning about population regulation from yearly surveillance data is that several factors other than population size influence the number of ticks collected per sample. For example, ambient temperature influences tick activity, and thus efficiency of flag sampling. The relationship between the number of ticks per sample and ambient temperature is shown, for each sample year, in Table 1. Significant positive correlations occurred only when ambient temperatures reached below 20° C (in 1993 and 1994). Therefore, temperatures below 20° C suppress questing activity. Furthermore, the timing of sampling relative to tick phenology influences the number collected. Note the low population size recorded in 1993 (when sampling was early in the season) and in 1987 and 1995 (when sampling was late in the season) (Fig. 1, Table 1): Nymphal phenology at a site near the Fire Island Lighthouse (modified from Ginsberg & Zhioua 1995) is given for comparison (Fig. 4). At the Lighthouse

Figure 2. DEER POPULATION TREND AT TALISMAN, FIRE ISLAND
(from O'Connell & Sayre 1989, and Underwood pers. comm.)

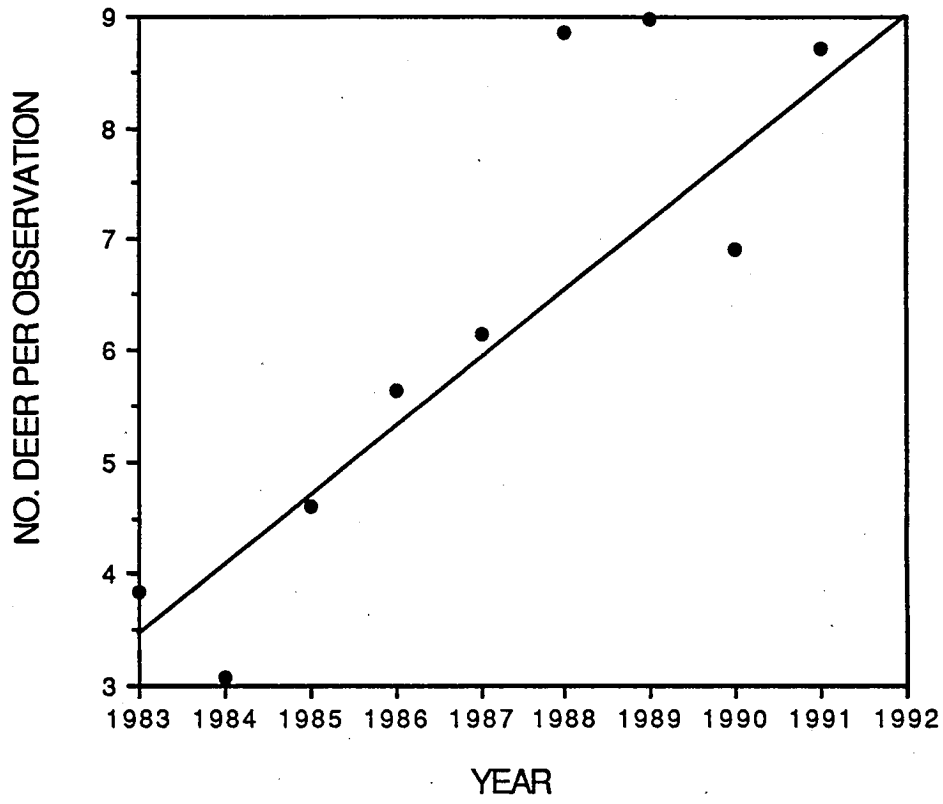


Figure 3. KEY FACTOR ANALYSIS, NYMPHAL *Ixodes scapularis* AT TALISMAN, FIRE ISLAND NATIONAL SEASHORE

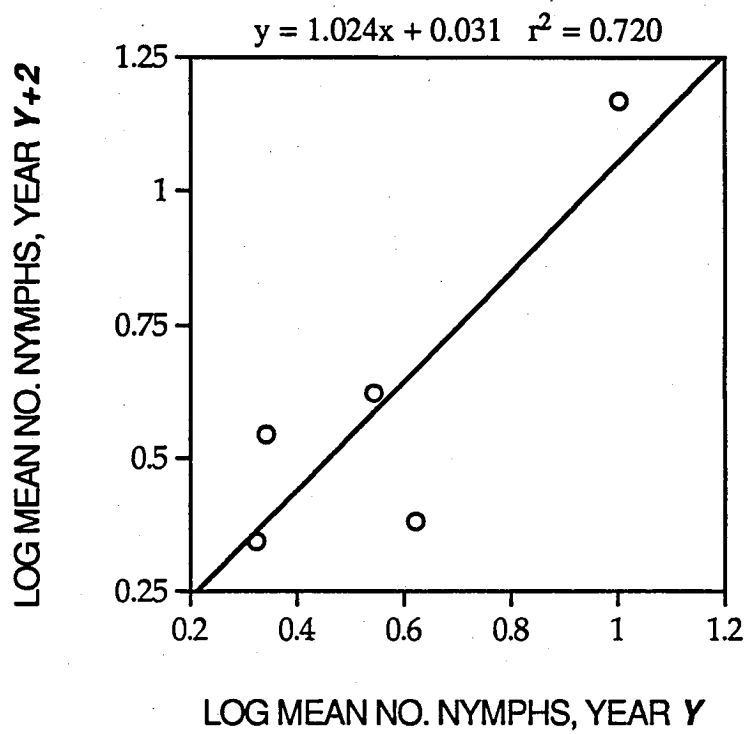


Figure 4. PHENOLOGY OF NYMPHAL *Ixodes scapularis*
AT THE LIGHTHOUSE TRACT, 1995

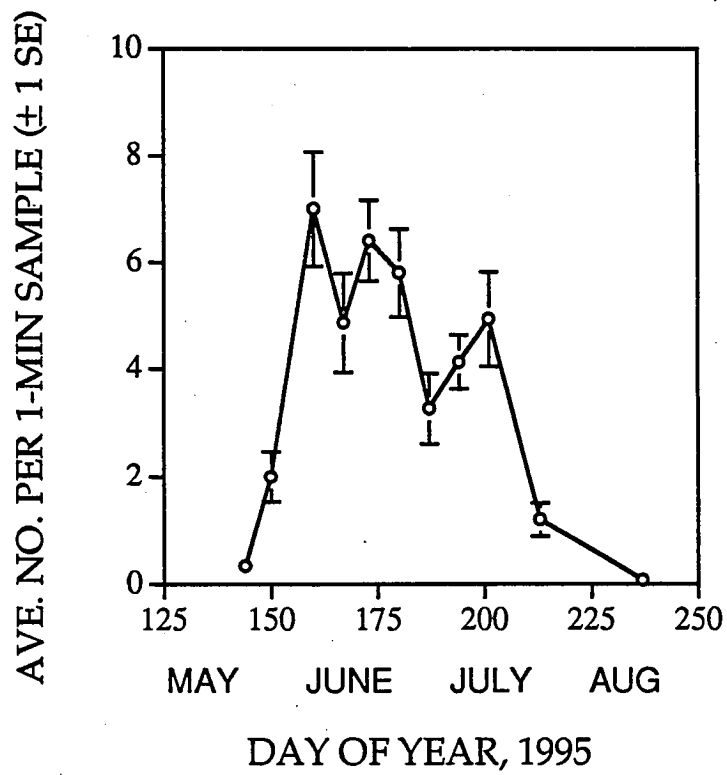


Table 1. Relationship of tick activity to ambient temperature.

Correlation coefficient (*r*) and significance (*P*) of relationship between number of ticks per sample and ambient temperature (* only one temperature reading per day in 1987-1989).

Year	Temperature range (°C)	No. samples	Sample dates	<i>r</i>	<i>P</i>
1987	26-29 *	18	7/10-11	0.175	0.486
1988	21-25 *	10	6/28-7/6	0.194	0.591
1989	23-27 *	15	6/12-7/4	- 0.182	0.516
1991	20-24	12	6/14-27	0.096	0.766
1992	21-24	15	6/10-11	- 0.203	0.468
1993	15-20	26	5/28-29	0.678	0.0001
1994	19-24	15	6/7-8	0.606	0.017
1995	21-24	15	7/11-12	- 0.537	0.039

Tract, where samples were taken at the same time of year in 1994 and 1995, nymphal populations were comparable in both years. This result differs markedly from the Talisman data (Fig. 1) where samples in 1994 were taken at a different time of year than in 1995. These factors complicate interpretation of the Talisman data. Any conclusions about tick population regulation are therefore tentative, and require independent confirmation.

Table 2. Prevalence of *Borrelia burgdorferi* infection in nymphal *Ixodes scapularis* at Talisman, Fire Island National Seashore, NY.

Year	Number of nymphs tested	% infected
1992	147	20.4%
1993	106	15.1%
1994	218	28.4%
1995	32	25.0%

Infection rates of *I. scapularis* nymphs with *B. burgdorferi* from 1986 to 1991 were reported by Ginsberg (1991) and from 1992 to 1995 are presented in Table 2. For Table 2, ticks were tested for infection by DFA. Infection rates in nymphs ranged from 15.1% in 1993 to 32.1% in 1986. This range is comparable to prevalences reported by other authors at other northeastern sites (Anderson 1988).

Chapter 2. Natural enemies of *Ixodes scapularis*

Numerous vertebrate species sometimes eat ticks (Jenkins 1964), but their roles in tick population regulation have never been evaluated. Recent studies of predation by helmeted guineafowl on lawns have shown only limited effects on *I. scapularis* populations (Duffy et al. 1992). Invertebrate predators, such as ants and spiders, also sometimes eat ticks, but our knowledge is limited to anecdotal observations (Fish 1993, Wilson & Deblinger 1993).

The parasitoid wasp, *Hunterellus hookeri* (Hymenoptera: Encyrtidae), attacks *I. scapularis* but does not control tick populations. In fact, this wasp is only found where ticks are extremely abundant (Mather et al. 1987, Hu et al. 1993).

Numerous species of pathogenic fungi, bacteria and viruses have been reported from ticks (Roberts et al. 1983), but there is little specific information about pathogens of *I. scapularis*. In this chapter, preliminary results are reported on screening trials of several potential predators and pathogens of *I. scapularis*.

Predatory arthropods

Leaf litter-dwelling arthropods were obtained by collecting samples of leaf litter in quart-size ziploc bags at Talisman, Fire Island, NY and extracting arthropods using modified Berlese funnels in the Talisman laboratory facility. Specimens were forced from litter by incandescent light bulbs above the funnels, and were collected beneath the funnels in jars with moist filter paper, and with the top rim smeared with petroleum jelly to prevent escape. Predatory and omnivorous arthropods were placed in chambers with immature *I. scapularis* that had been collected by flagging in the Talisman area. Chambers were 150 x 25mm Integrid tissue culture dishes (Becton, Dickinson & Co., Cockeysville, MD), with filter paper on the base, and sealed with masking tape. Chambers were checked after 24 hours to determine whether litter arthropods had consumed ticks. Ambient temperature and humidity were recorded with a hygrothermograph. Chambers were set and collected on 18-20 and 26-28 June, and on 1-3, 16-18 and 24-25 July 1991.

The tick predator screening trials are listed in Table 3. Several taxa of predatory arthropods were screened, as well as several omnivorous taxa, and some taxa that are not normally considered predators. All of the ticks in the chambers were alive after 24 hours, with the exception of one larval tick which was missing in the chamber with a cricket (Chamber 3 on 18 July 1991). None of the leaf litter-dwelling arthropods were voracious-enough feeders on ticks in these trials to suggest that they might show potential as biological control agents for *I. scapularis*.

Table 3. Screening trials for leaf litter arthropods as predators of *Ixodes scapularis* immatures, 1991.

Dates	Chamber #	Arthropod	# ticks	date ticks collected
18-20 June	1	Heteroptera	3 nymphs	14 June
	2	Pseudoscorpion	3 nymphs	14 June
	3	Collembola	3 nymphs	14 June
	4	Insect larva (Coleoptera?)	3 nymphs	14 June
	5	Collembola	3 nymphs	14 June
	6	Acari	2 nymphs	14 June
	7	Acari	3 nymphs	14 June
26-28 June	1	Hymenoptera (wingless)	3 nymphs	14 June
	2	Acari	3 nymphs	14 June
	3	Acari	3 nymphs	14 June
	4	Araneae	3 nymphs	14 June
	5	Chilopoda	3 nymphs	14 June
	6	Araneae	3 nymphs	14 June
	7	Formicidae	3 nymphs	20 June
1-3 July	1	Isoptera	2 nymphs	27 June
	2	Gryllidae	2 nymphs	27 June
	3	Diplura	2 nymphs	27 June
	4	Hymenoptera (parasitic)	2 nymphs	27 June

Table 3. continued -

1-3 July	5	Diptera	2 nymphs	27 June
16-18 July	1	Coleoptera (larva)	3 larvae	16 July
	2	Formicidae	3 larvae	16 July
	3	cricket	3 larvae	16 July
	4	Isoptera	3 larvae	16 July
24-25 July	1	Acari	3 larvae	16 July
	2	Acari	3 larvae	16 July
	3	Acari	3 larvae	16 July
	4	Acari	3 larvae	16 July
	5	Insect larva (Coleoptera?)	3 larvae	16 July
	6	Acari	3 larvae	16 July
	7	Formicidae	3 larvae	16 July
	8	larva	3 larvae	16 July

Pathogenic nematodes

Several groups of nematodes are pathogenic to arthropods (Poinar 1979). In particular, nematodes in the families Steinernematidae and Heterorhabditidae have been shown to be pathogenic to ticks (Samish & Glazer 1991, 1992, Glazer & Samish 1993, Mauleon et al. 1993). Recent studies have shown that *Steinernema carpocapsae* and *S. glaseri* (Steinernematidae) are pathogenic to *Ixodes scapularis* in the laboratory (Zhioua et al. 1995). The nematodes are pathogenic to engorged female *I. scapularis*, but not to immatures or unengorged ticks, possibly because the nematodes enter via the genital pore of the female, which is partly everted in the engorged tick. Unfortunately, although these nematodes are pathogenic to the ticks, they do not complete their life cycles in intact ticks. Furthermore, mortality of infected ticks is greatest between 20° and 30° C., and lower at 15° C. Unfortunately, ambient temperatures are below 20° C during much of the active period of adult female *I. scapularis* in the northeastern U.S. (Zhioua et al. 1995). Nevertheless, these nematodes may be useful as biological control agents for *I. scapularis* under certain specialized conditions (e.g., in animal stalls in barns).

Pathogenic fungi

Entomopathogenic fungi sometimes infect ticks, including close relatives of *I. scapularis*, such as the European species *I. ricinus* (Samsinakova et al. 1974, Kalsbeek et al. 1995). In 1993, we surveyed and isolated pathogenic fungi from *I. scapularis* collected by flagging on Fire Island. Individual ticks were held in sterile petri dishes on separate Whatman 7.0 cm filter paper dipped in sterile, double distilled H₂O at 25° C and topped with parafilm (to ensure 100% humidity) for 7 days. Fungi growing on tick cadavers were cultured in standard petri dishes that contained Sabouraud dextrose agar plus 1% yeast extract (SDAY) and held at 25° C with a photoperiod of 16:8 L:D h. Single spore cultures were subsequently propagated on the same medium.

The fungi reared on SDAY were passed approximately 10 times on the medium before pathogenicity trials. Conidia and hyphae were collected by scraping the surface of each colony with a sterile spatula. Ten ml of sterile H₂O was added to the scrapings and conidia were filtered through a nylon mesh cloth. Conidial concentrations were determined using a hemacytometer, and then diluted to 10⁸ conidia per ml.

Conidia were applied to ticks in two ways. First, a Potter spray tower was used to apply ultralow volume spray onto the surfaces of test ticks (10 engorged larvae in each trial). About 3 ml was sprayed onto ticks in a petri dish. The dishes were sealed with parafilm after spraying and incubated for 7d. An aliquot was also applied to SDAY to estimate percent germination. Second, conidia were applied by immersing ticks for 30 s in a conidial suspension ($\leq 10^8$ conidia/ml) and then drawing off the suspension by absorption onto filter paper. Each treated tick was placed in a petri dish sealed with parafilm and incubated for 7 d. Samples of the conidial suspension were applied to SDAY plates to estimate percent germination (after 24 h). Percent mortality of ticks was recorded daily. A treatment with double distilled H₂O served as a control.

Two entomopathogenic species were isolated from *I. scapularis* collected on Fire Island, *Beauveria bassiana* (Balsamo) and *Verticillium lecanii* (Zimmerman). Both fungal species were pathogenic to *I. scapularis*. Spore germination averaged 92.5% for *B. bassiana* (10 replicates) and 90.8% for *V. lecanii* (5 replicates). Tick mortality by the spray tower method was 86% for both fungal species, and by the conidial suspension method was 82% for *B. bassiana* and 90% for *V. lecanii*. There was no mortality among the controls. Therefore, entomopathogenic fungi show considerable promise as biological control agents for *I. scapularis*. Screening of other pathogenic fungi, comprehensive pathogenicity trials, and development of suitable delivery systems are needed before fungi can be utilized as biological control agents against *I. scapularis*.

Chapter 3. An apparatus to study tick orientation and host-seeking behavior

Host-seeking behavior by ticks can be divided into three phases (Lees 1948, Camin 1963): 1) *passive phase* - movement to an appropriate questing site and waiting for a host; 2) *questing phase* - recognition that a potential host is present, orientation and grasping onto the host; and 3) *host-discrimination phase* - attachment and feeding, or rejection and dropoff. In this study, we concentrate on phase 1) the passive phase. To find an appropriate questing site, a tick must find appropriate habitat, and then select a site where the tick is likely to encounter a host. Therefore, two behaviors are potentially required in the passive phase; habitat selection and questing site selection. These may require separate orientation mechanisms, or may be a continuous process with a single set of orientation cues, depending on the type of habitat and questing site utilized by the tick species.

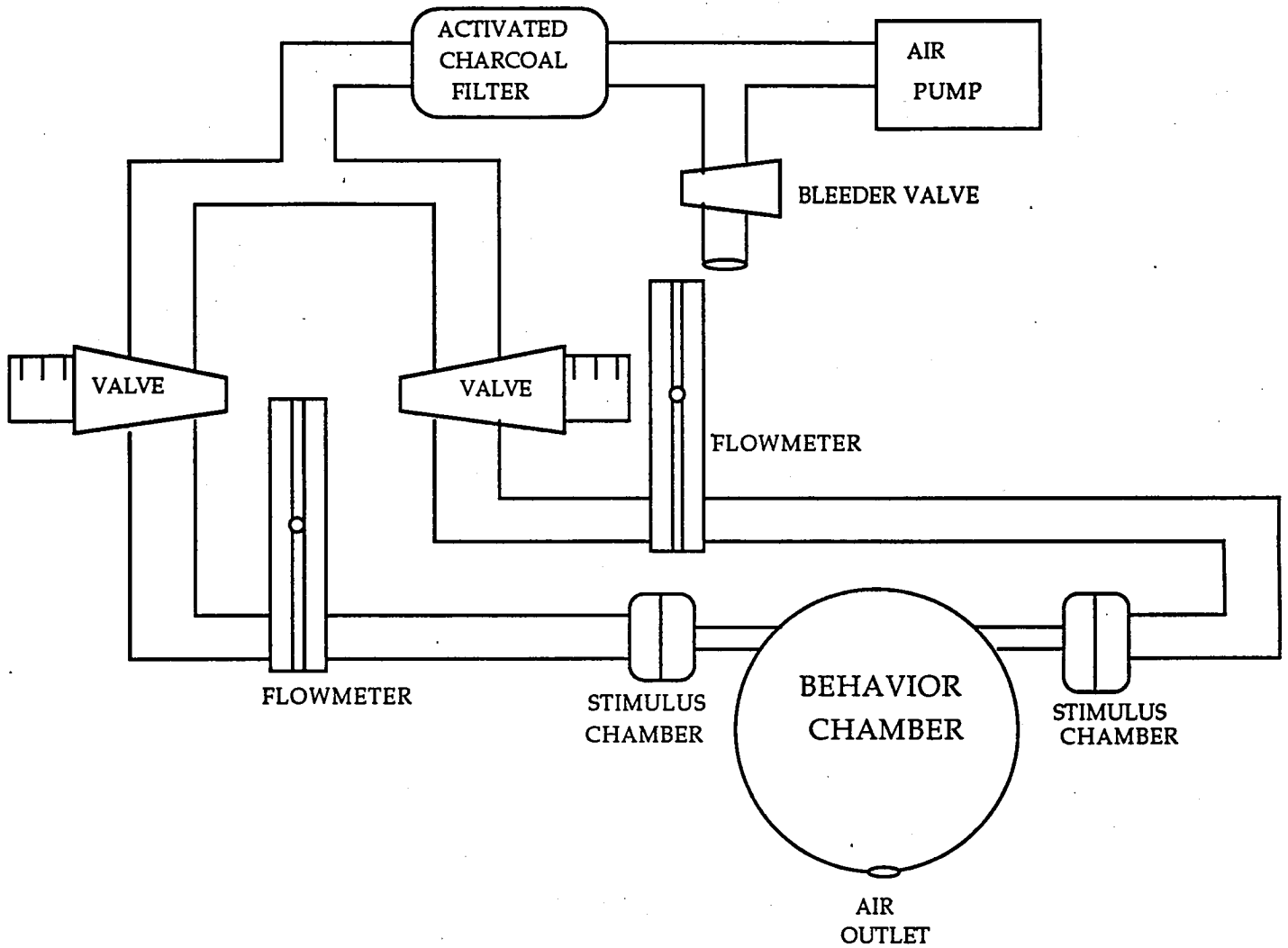
Ticks respond to a great variety of orientation cues while seeking hosts, including light (Wilkinson 1953, George 1963), humidity (Sonenshine 1963), gravity (McEnroe & McEnroe 1973), sound (Webb et al. 1977), CO₂ (Garcia 1962, 1969, Nevill 1964), various pheromones (Leahy et al. 1973, Wood et al. 1975, Sonenshine 1991), and other stimuli, often in complex combinations that result in efficient orientation to specific types of host animals (Lees 1948, El-Ziady 1958, Howell 1972, Waladde & Rice 1982). Furthermore, the response by a tick to a given environmental stimulus at any given time depends on the recent history and physiological state of the tick, such as the state of hydration (Lees 1948) or environmental conditions on the previous day (McEnroe & McEnroe 1973).

Among ticks in the *Ixodes ricinus* complex, the responses to environmental stimuli have been studied in *I. ricinus* (Aeschlimann 1972, Gigon 1985), but very little attention has been paid to host-seeking behavior in its North American relatives. Lane et al. (1995) studied the questing activity of *I. pacificus* in relation to environmental factors, and Carroll et al. (1995) demonstrated behavioral responses of *I. scapularis* to secretions from external glands of white-tailed deer. In this chapter we describe an olfactometer apparatus that we developed to test behavioral responses of *I. scapularis* to various environmental cues.

Olfactometer apparatus

The tick behavior apparatus is shown in Fig. 5. Air flow is supplied by an air pump (Budget Dyna-pump, 10 psi), passes through an activated charcoal filter, and divides at a T-juncture into two vinyl tubes through which flow is adjusted by capillary valves that lead to flowmeters in each airway. The two tubes lead to stimulus chambers (in-line filter holders) that lead, in turn, to two input holes into the behavior chamber. An air outlet hole (covered with fine mesh) is located at the opposite end of the behavior chamber. The behavior

Figure 5. TICK BEHAVIOR APPARATUS

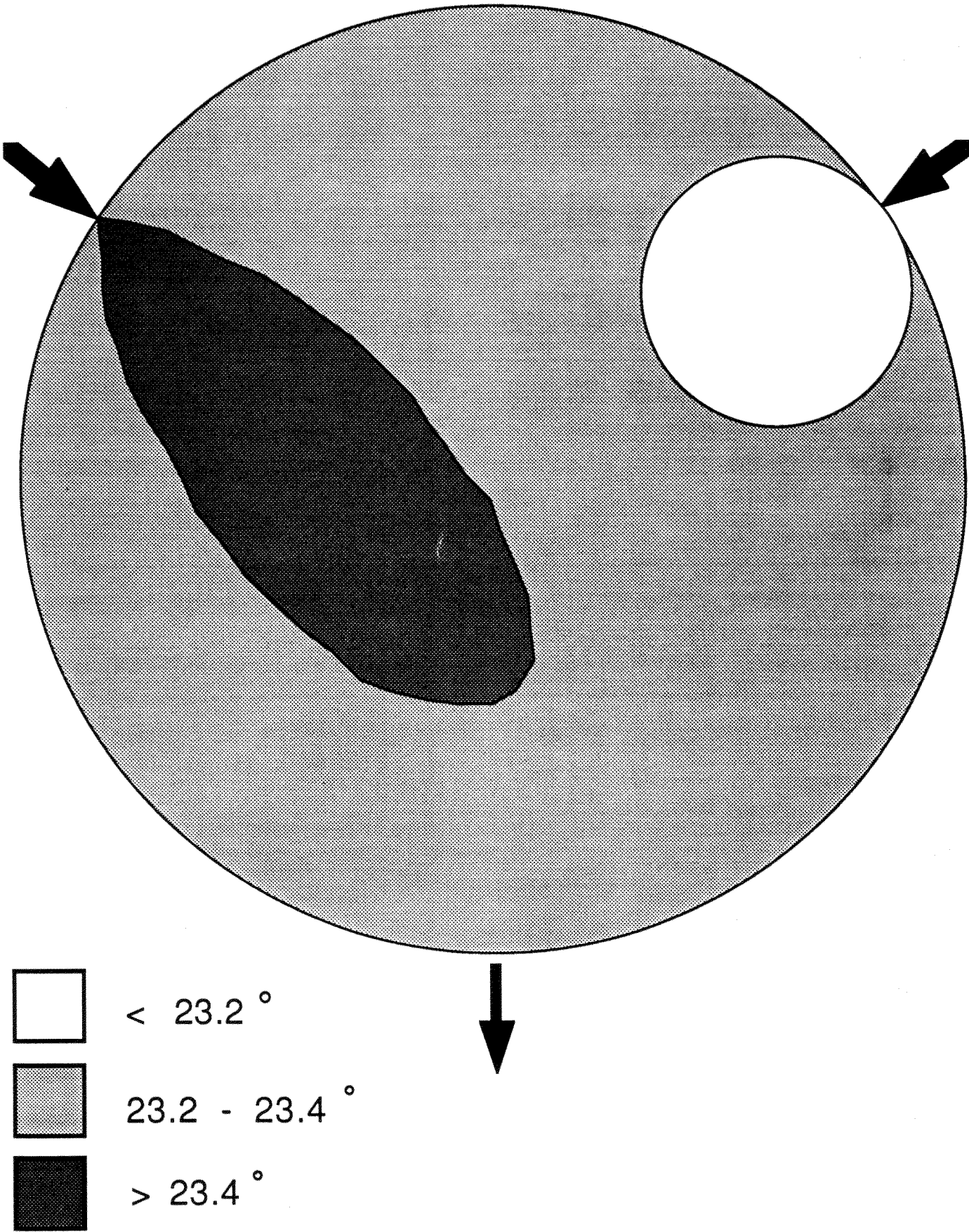


chamber was modified from a 150 x 25mm Integrid tissue culture dish (Becton, Dickinson & Co., Cockeysville, MD).

The reason for using a chamber, rather than a Y-tube or other apparatus, is that *I. scapularis* seeks host near ground level. Narrow chambers with concave inner surfaces (like Y-tubes) mimic nests, and may be appropriate for studies of nest-dwelling ticks, but may produce inappropriate behavior in free-living ground-dwelling species. Chambers with vertical posts may be appropriate for species that quest up in vegetation, but may produce aberrant behavior in ground-questing species. For ground (or near ground) questing ticks such as *I. scapularis*, a flat surface is more likely to produce natural questing-site seeking behavior.

Preliminary trials with the chamber apparatus suggested a further problem. Ticks could be observed moving through the chamber in various patterns, but these movement patterns could not be interpreted unless the distribution of gasses in the chamber was known. An observer cannot know if a tick is turning in response to a given odor stimulus, unless he/she knows whether the tick is encountering that odor at the time. Therefore, we designed a test to determine the distribution of gasses in the chamber, by running warm air through one of the input holes, and measuring the distribution of temperatures in the chamber using a needle temperature probe (connected to a Tri-sense meter) inserted through small holes in the bottom of the chamber. The distribution of temperatures resulting from warm air entering through the left-hand chamber input hole is shown in Fig. 6. A plume of warm air is apparent around the warm-air input hole to the chamber, with cool air near the other input hole. Additional trials are planned using smoke entering through a single input hole to confirm the results using warm air, to test whether the distribution of gasses is the same with no holes in the bottom of the chamber, and to determine whether the plume changes with minor disturbances of the apparatus (e.g., moving the vinyl tubes). Once these tests have been completed, the chamber will be ready for orientation experiments that examine responses to inputs (such as odors of different types of leaves) from single input holes, for bioassays of potential tick repellents, for pheromone studies, and other behavioral experiments.

Figure 6. TEMPERATURE DISTRIBUTION IN TEST CHAMBER



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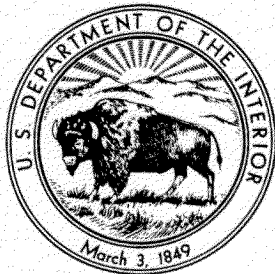
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As the nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural and cultural resources. This includes fostering wise use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people. The department also promotes the goals of the Take Pride in America campaign by encouraging stewardship and citizen responsibility of the public lands and promoting citizen participation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

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