Host-produced chemicals appear to play important roles in mediating behaviors that help ticks locate and contact suitable hosts. Host-generated carbon dioxide elicits a range of responses, from leg extension to attraction, from host-seeking ticks (Waladde and Rice 1982, Sonenshine et al. 1986). Some species of ticks have been reported to recognize chemical residues left on vegetation and substrate and to wait on or near these residues to ambush hosts (Rechav et al. 1978; Carroll et al. 1995, 1996).

The blacklegged tick, *Ixodes scapularis* Say, lone star tick, *Amblyomma americanum* (L.), and the American dog tick, *Dermacentor variabilis* (Say), are widespread in the eastern half of the United States. These ticks readily bite humans, and all are considered to be of public health importance as vectors of Lyme disease, mononuclear ehrlichiosis, and Rocky Mountain spotted fever, respectively (Sonenshine 1993). As adults, all 3 species of ticks will feed on a variety of medium-sized to large mammalian hosts. Strong relationships between population densities of lone star and black-legged ticks and their principal host the white-tailed deer, *Odocoileus virginianus* (Zimmermann), have been demonstrated (Wilson et al. 1985, 1988, 1990; Haile and Mount 1987). White-tailed deer have been reported as hosts of adult *D. variabilis* (Bishopp and Smith 1938), but such associations may be incidental. For instance, Bloemer et al. (1988) reported finding no American dog ticks on any of 97 white-tailed deer.

Among *A. americanum*, *D. variabilis*, and *I. scapularis*, the 1st mentioned is best described as a hunting type (Waladde and Rice 1982), whereas *I. scapularis* is an ambush type as *D. variabilis* also tends to be (Smith et al. 1946). However, all 3 species ambush hosts from vantage points on vegetation, although they appear to vary in the way in which ambush contributes to host-acquisition. In nature, host-seeking ticks are exposed to chemical residues left by a variety of vertebrate species, hosts and nonhosts. The purpose of this study was to ascertain the responses of *A. americanum* and *D. variabilis* in terms of arrestment (as on vantage points for ambushing hosts) to residues associated with the pelage of principal hosts, and to assess the responses of all 3 species of ticks to pelage substances from a species considered a minor host.

**Materials and Methods**

Ticks. Adult ticks were collected by flagging in Queen Anne’s and Prince George’s Counties in Maryland. Ticks were maintained under photoperiod and temperature regimes corresponding to their seasons of host-seeking activity. *I. scapularis* adults were maintained at 6°C, ~99% RH, and a photoperiod of 11:13 (L:D) h. *A. americanum* and *D. variabilis* adults were held at 22°C and a photoperiod of 16:8 (L:D) h in plastic shell vials with perforated caps inside capped 50-ml centrifuge tubes containing 2 ml of a saturated potassium nitrate solution to maintain ~95% RH (Winston and Bates 1960). *I. scapularis* adults were collected from mid-October to early December, and *A. americanum* and *D. variabilis* were collected from mid-May to mid-July. Adult *I. scapularis* were held up to 5 mo and *A. americanum* and *D. variabilis* up to 3 mo at the time of testing. All trials involving deer glands were conducted when the cohort of the ticks tested...
were seeking hosts in nature. The exact time that elapsed between when the ticks molted and they were tested is unknown. In the case of D. variabilis it is possible a small percentage of individuals may have been survivors from the previous year’s cohort (Sonenshine et al. 1966). Individual ticks were selected for testing based on their physical integrity (e.g., no missing appendages) and their motility when removed from the storage vial.

Substances. Samples of substances associated with canine pelage were obtained by rubbing clean glass rods (12 cm long, 0.3 cm diameter) on the dorsal surface of dogs’ ears. Samples of canine coat substances were obtained from cooperating dog owners who followed the procedure described. Glass rods were handled only by persons wearing clean vinyl gloves. The glass rod samples were refrigerated at 5°C until used (24–48 h later) in the behavioral bioassays. Samples from tarsal glands of white-tailed deer were obtained from freshly hunter-killed animals by carefully excising the gland and associated pelage to avoid contamination of the pelage with blood, or by removing the lower portion of the leg at a point just above the tarsal gland. The glands were immediately placed in plastic bags and stored at −15°C. Because adults of I. scapularis seek hosts in the fall and spring and adults of A. americanum and D. variabilis seek hosts in spring and summer, the tarsal gland samples tested had been obtained in November and early December and in late March and early April. All spring gland samples were from deer that were taken under a Crop Damage Permit or a Wildlife Permit issued by Maryland Department of Natural Resources. Frozen tarsal gland samples retain kairomonal activity for ~4 yr in bioassays with I. scapularis (J.F.C., unpublished data) so a given spring sample may have been older than a given fall sample and in other instances the reverse was true.

Experiments. Arrestance behavior was assessed by releasing a single tick on a roughly rectangular block of modeling clay (Prang, American Crayon, Sandusky, OH) extending across a plastic petri dish (3.5 cm diameter by 1 cm high). A vertical glass rod that had been rubbed on canine ear pelage or rubbed between the thumb and forefinger of a vinyl-gloved hand that had rubbed the pelage associated with a deer tarsal gland was inserted at 1 end of the clay block. A 2nd glass rod that had rubbed the pelage associated with a canine ear pelage or rubbed between the thumb and forefinger of a clean vinyl glove and inserted vertically at the opposite end of the clay block (~2.5 cm from the treated rod) (depicted in Carroll 1998). Before a tick was released on the clay block midway between the rods, water was added to the petri dish, and the dish was placed in a petri dish (10 cm diameter, 1.5 cm high), also containing water, inside a Plexiglas glove box (65 by 85 by 45 cm) that contained water =1 cm deep. The water confined the tick to the clay block and the rim of the petri dish, and kept the relative humidity inside the glove box at ~95%. Temperatures inside the glove boxes were 21–25°C during testing. The location of the tick was recorded at 1, 15, and 24 h after its release. Ticks that fell or crawled into the water were replaced on the clay island until 18 h after their release. To account for the possible influence of position or lighting on the outcome of the bioassays, the locations of treatment and control rods in relation to the front of the glove box were reversed for every 5 ticks tested.

Ten A. americanum and 10 D. variabilis of each sex, and 10 I. scapularis females were tested against substances rubbed from the ears of each of 3 dogs (male pit bull, German shepherd, and collie, n = 30 for each sex of each species of tick). Ten A. americanum and 10 D. variabilis of each sex were tested against each of 3 deer tarsal gland samples from the fall. Because adult A. americanum and D. variabilis seek hosts in the spring, the same ticks were used 1–2 wk later in trials against 3 spring samples. Ten female I. scapularis were tested against each of the 6 deer tarsal gland samples used with the A. americanum and D. variabilis. In some cases a group of ticks was tested first against substances from spring tarsal glands and then against fall, and in other cases the reverse was true. As a direct comparison between fall and spring glands and using the same bioassay, A. americanum females were given the choice between a rod treated with substances rubbed from a fall gland and a rod with spring gland substances on it. After each test the clay island/petri dish units were washed with soap and water and thoroughly rinsed with water. The glass rods were washed with soap and water, rinsed with water, and wiped with a tissue soaked in acetone and another tissue soaked in methanol. Data were analyzed by chi-square $\chi^2$ contingency tables, with responses of each tick considered independent.

Results

Usually within minutes after its release, a tick crawled about the rim of the petri dish and the clay base and ascended and descended the glass rods. This activity continued off and on for hours, but by the following morning activity was minimal. The location of ticks at 18 h after their release differed little from 24 h after release.

Canine ear samples elicited an arrestance response among all species and sexes of ticks tested (Table 1). At 24 h after their release on the clay blocks, male

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Table 1. Number of ticks on glass rods rubbed on dorsal surface of dogs’ ears and on untreated control rods 24 h after ticks were released on clay blocks with the 2 glass rods

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>Control</th>
<th>$\chi^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. scapularis</td>
<td>Female</td>
<td>25</td>
<td>1</td>
<td>18.742</td>
</tr>
<tr>
<td>A. americanum</td>
<td>Female</td>
<td>26</td>
<td>2</td>
<td>18.491</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>28</td>
<td>2</td>
<td>21.675</td>
</tr>
<tr>
<td>D. variabilis</td>
<td>Female</td>
<td>23</td>
<td>6</td>
<td>9.085</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>28</td>
<td>2</td>
<td>21.675</td>
</tr>
</tbody>
</table>

Thirty ticks of each species and sex tested individually against samples from 3 dogs. Treatments and controls may total <30 because some ticks remained on clay block or fell in water moat.
A high level of male (93.3%) and female (86.7%) *A. americanum* responded to all spring gland substances (Carroll et al. 1995). Male *D. variabilis* were similarly responsive to spring gland substances, and *D. variabilis* were similarly responsive to canine ear pelage substances. Most (80%) male *A. americanum* became akinetic within 1 h on glass rods treated with deer or canine residues and these ticks plus others were akinetic on the treated rods 23 h later, which suggests that the response to the host-produced chemicals was more than transitory. The arrestant responses of *A. americanum* and *D. variabilis* to deer and canine kairomones may also occur under natural conditions and do so in an adaptively significant way. Inasmuch as the mammalian hosts tend to be creatures of habit, it is of adaptive value for a tick to locate itself on a vantage point on or near host-produced kairomonal residues on vegetation or the substrate, because host species are likely to visit the spot regularly. The reported occurrence and retention of host-seeking adult *D. variabilis* along trails (Newhouse 1983, Carroll et al. 1991) supports the scenario that they use chemical cues to locate host-ambushing sites.

### Discussion

Arrestant responses by female *I. scapularis* to chemicals associated with external deer leg glands in laboratory bioassays (Carroll et al. 1995) have been verified in the field, where both females and males became akinetic on bamboo skewers rubbed with leg gland substances (Carroll et al. 1996). In the current study, *A. americanum* showed a strong arrestant response to deer tarsal gland substances, and *D. variabilis* were similarly responsive to canine ear pelage substances. Most (80%) male *A. americanum* became akinetic within 1 h on glass rods treated with deer or canine residues and these ticks plus others were akinetic on the treated rods 23 h later, which suggests that the response to the host-produced chemicals was more than transitory. The arrestant responses of *A. americanum* and *D. variabilis* to deer and canine kairomones may also occur under natural conditions and do so in an adaptively significant way. Inasmuch as the mammalian hosts tend to be creatures of habit, it is of adaptive value for a tick to locate itself on a vantage point on or near host-produced kairomonal residues on vegetation or the substrate, because host species are likely to visit the spot regularly. The reported occurrence and retention of host-seeking adult *D. variabilis* along trails (Newhouse 1983, Carroll et al. 1991) supports the scenario that they use chemical cues to locate host-ambushing sites.

In contrast to *A. americanum* males, which responded to all tarsal gland samples, *A. americanum* and *I. scapularis* females and male and female *D. variabilis* showed rather variable responses. Female *I. scapularis* and male *D. variabilis* responded strongly to spring tarsal gland samples, but appeared to avoid 2 of the fall samples (0 of 20 *I. scapularis* and 3 of 20 *D. variabilis*) and to respond to samples from the same 3rd deer (8 of 10 *I. scapularis* and 10 of 10 *D. variabilis*). Arrestant responses to fall tarsal gland substances from male and female deer have been substantiated in previous studies (Carroll et al. 1995, 1996); therefore, it seems likely that individual variation among the deer may account for the differing responses to fall samples in this study. The concentrations of behavior-mediating chemicals possibly varied among the samples. White-tailed deer...
urinate on their tarsal glands (Marchinton and Hirth 1984) and in some circumstances, I. scapularis adults avoid deer urine (Carroll 1998). Other possible sources of variability were the age of the ticks tested and the age of the samples, although the 2 fall samples to which there was no response were the newest and oldest samples tested. Tick responses to stimuli, such as carbon dioxide, are known to change as they age.

Adult I. scapularis, A. americanum, and D. variabilis exhibited arrestant responses to substances associated with the pelage of a species not considered a principal host (A. americanum and I. scapularis to canine substances and D. variabilis to deer substances). Although white-tailed deer have been reported to be hosts of adult American dog ticks (Bishop and Smith 1938), a strong relationship between deer and adult D. variabilis populations has not been demonstrated (Bloemer et al. 1988). Perhaps adult D. variabilis cannot discriminate, possibly to their detriment, among chemical residues left by a variety of mammalian species, and will wait on or near any such residue. However, deer trails are avenues of transit not only for deer, but also for a variety of medium-sized mammals, and it might benefit all 3 species of host-seeking ticks to recognize deer-produced chemicals and wait along deer trails.

According to Hölldobler and Wilson (1990), a kairomone is a substance, or blend of substances, emitted by an organism that elicits a response adaptively favorable to the receiver but not to the emitter. Crude deer leg gland substances may not conform exactly to Hölldobler and Wilson’s (1990) definition of a kairomone, inasmuch as the glands are thought to produce pheromones that influence deer behavior. Although the distance from glandular residues at which ticks respond to host-mediating chemicals has yet to be established, these findings suggest the possibility of a tick-arrestant chemical that influences tick host-ambush site selection and is common to both dogs and deer. An alternative explanation is that multiple compounds in host-pelage substances elicit arrestant responses in ticks and that ticks respond to a range of compounds. Steullet and Guerin (1994) identified several compounds common to both rabbit and steer odors that stimulate olfactory sensilla in Haller’s organ of the tropical bont tick A. variegatum Fabricius. Further research is warranted to isolate and identify kairomonally active compounds shared by deer and dogs, and possibly other mammals. Kairomones may be used to mediate tick behavior in ways to reduce risk of tick bite to humans and domestic animals. For example, host-seeking ticks could be trapped with kairomonal lures or induced to select ambush sites away from areas frequented by humans.

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