Tick Host-Seeking Behavior

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Abstract: Ticks are parasitic chelicerate arthropods that are capable of transmitting several medically important diseases such as Lyme disease. The host-seeking behavior of various members of the family Ixodidae is reviewed, beginning with an introduction to the taxonomy and physiology of ticks. Host-seeking ticks are attracted to the CO₂ and kairomones emitted by potential hosts, detected by Haller’s organs located on the first tarsus of the forelegs. Carbon dioxide attraction has been exploited as a method for capturing and sampling ticks for several years, the methodology has changed little since its introduction. Most of the kairomonal work has been performed on blacklegged ticks and their hosts, white-tailed deer. Kairomonal response is typically host specific; ticks react to substances excreted by interdigital glands and possibly to host urine deposited on vegetation along game trails. Ticks have been found to alter questing height in response to the average height of the local host population and will alter that height as the host species tends towards different heights across its geographical range. Attachment site of the same tick species has been found to vary with different host species, possibly in response to light exposure. Another study found no significant difference between tick density alongside of and away from trails. Several studies examined the effects of temperature and humidity on tick activity and host-seeking behavior. It was found that using gross meteorological measurements provided by weather centers is not an effective method of predicting tick activity. Instead, tick activity is dependent upon microenvironmental and micrometeorological measurements of temperature and humidity. Measurements taken near and within the soil or litter layer are better indicators of host-seeking behavior. Ticks are also not distributed randomly throughout potential habitat. The majority of ticks are found in “hot-spots” of activity, whether near a host trail or not. These areas have more ticks because the temperature and humidity conditions are ideal. These topics and the articles they are from are discussed in further detail in this review.

Introduction

Just as squares are rectangles, ticks, technically are mites, although very large ones. They are chelicerates in the class Arachnida and order Ixodida, possessing four pairs of walking legs in the adult stage, pedipalps, and chelicerate mouthparts. The body is composed of two regions, the gnathosoma and idiosoma. The gnathosoma is anterior
and contains the head and mouthparts. The idiosoma comprises the rest of the body and is sac-like (Walter & Shaw 2005). The physical development of the life cycle begins with the egg, then moves to six-legged larvae, on to one or more nymphal instars (depending on species) with eight legs, and finally an eight-legged, sexually mature adult (Klompen 2005). The members of the two families of ticks, Ixodidae and Argasidae, differ somewhat in their life cycles. Ixodidae larvae seek and feed on the blood of hosts for 3-7 days, the final day contributing to almost half of the body mass increase of the tick. The larva drops off the host and molts into a nymph, which then finds another host and feeds for 3-8 days, after which it too drops off and molts into the adult. Mating can take place on or off a host depending upon species. Most Argasidae larvae seek out and feed upon a host for 3-8 days, similar to Ixodidae. Engorged larvae drop off and molt into the first nymphal instar. Each subsequent instar feeds and drops off a host before molting. Adults and nymphs feed for less than an hour. Mating is conducted off-host (Klompen 2005).

Ticks are obligate parasites, living completely off of the blood of vertebrates. Many bird and reptile species and almost every mammal species have a tick associated with it. Unlike many parasites, ticks drop off of the host after each blood meal, which requires they seek out a new host each time they feed. Ticks may survive for up to a year without feeding and spend approximately 95% of their life off-host (Klompen 2005). In Ixodidae, the process of finding a host is known as questing behavior. Ixodids typically climb to host-height on vegetation and wait for a host to brush up against the foliage. When this occurs, the tick grabs onto the host attaches itself. Detection of hosts is
accomplished with the use of Haller’s organs located on the first tarsus of the forelegs. Haller’s organs detect both CO\(_2\) and kairomones emitted by potential hosts.

Aragasids, however, are nidicolous, living in the nests or burrows of their hosts, often feeding upon the same individual (Klompen 2005). These ticks do not need to seek out new hosts and therefore do not exhibit questing behavior. Because of the differences between the two families, most host-seeking behavior has been focused on Ixodidae.

Water loss is the most detrimental factor to ticks when off-host. Ixodids are found in microclimates with high humidity such as leaf-litter and soil. These ticks must return to this microclimate after feeding or if questing behavior is unsuccessful. Aragasids, on the other hand, are often found in much drier climates, occupying places such as caves and attics. The cuticle of Aragasids is much more leathery than that of Ixodids to prevent water loss (Klompen 2005).

Ticks are of importance to humans because they are vectors of disease. When a tick attaches to a host, it inserts an organ called a hypostome into the host’s skin to facilitate feeding. The hypostome is cemented into the skin with tick saliva and is the part of the ticks that remains embedded in the skin if the tick is removed improperly. Disease transmission is via the salivary gland secretion of infected ticks. Some of the diseases transmitted are Rocky Mountain spotted fever in the Rickettsia group, relapsing fevers, arboviruses such as Colorado Tick Fever, and the most studied, Lyme disease (Klompen 2005).

The types of articles reviewed in this paper focus on tick collection methods, response of ticks to host-specific kairomones, questing height and host attachment sites,
and temporal and climatic effects on host-seeking behavior. Because Argasidae exhibit little questing behavior, most of the articles are concerned with Ixodidae.

**Discussion**

*Collection Methods*

The most common method of collecting ticks in the field is by drag or flag sampling. Another, less used method is by trapping. Drag surveys are used to capture ticks exhibiting questing behavior and that have climbed up into the vegetation to await a suitable host. This method had been in use since the 1970s. The equipment used in a drag survey consists of a piece of sturdy cloth usually one meter² (Schulze et al. 2001), but may vary in size, such as 70X90 centimeters as used in a study by Schulze & Jordan (2003). A wooden dowel (approximately one cm diameter) is attached to the leading edge of the cloth and has a one-meter rope handle attached to each end. Two individuals pull the drag device, one on each end of the dowel and grasping the rope handle, through vegetation where ticks are collected on the cloth (Schulze et al. 2001 & Schulze & Jordan 2003). In the 2003 study by Schulze & Jordan, a steel rod was sewn into the trailing edge of the cloth for added weight. Several passes with the drag cloth are made through the vegetation, typically at different times of day and with the same “draggers”.

The problem with the drag method, is that it is difficult to perform and less effective when used in thick vegetation, under fallen branches, and around ornamental plants. In 1992, Carroll and Schmidtmann modified the drag method into what they refer to as the sweep method. Instead of two one-meter rope handles, their drag cloth had a 1.5-meter handle attached to one end of the leading edge dowel. The handle was angled upwards from the ground so that one operator could stand upright and “sweep” the device
underneath vegetation. Their method was just as effective as standard drag sampling for deer-tick nymphs \textit{Ixodes dammini} Spielman in open woodland habitat, and twice as effective at sampling in a dense, bushy habitat (Carroll & Schmidtmann 1992).

An additional method of collection is via carbon dioxide-baited trapping. Falco and Fish used CO$_2$ traps to determine the prevalence of deer ticks \textit{Ixodes dammini} Spielman in Westchester County, New York (1989). Their traps consisted of Styrofoam dry ice reservoirs with wooden bases. A 5mm hole was drilled on each side of the reservoir for CO$_2$ to escape and masking tape placed on the base to capture ticks attracted by the CO$_2$. In this study, a trap was placed at each corner of a 30X30m quadrat. Falco and Fish had five sites and trapped for 12 days and 16 nights, which yielded 919 tick larvae, 712 of which were from the same site. Two sites averaged only 7 ticks per night, while three sites averaged less than 1 tick per night (Falco & Fish 1989). No recent papers were found that used stationary CO$_2$ traps to sample ticks. This may be because questing ticks move little, preferring instead to wait for hosts to brush up against tick-occupied vegetation.

\textit{Kairomone Response}

Kairomones are pheromones emitted by one organism that attract another organism that negatively affects the emitter (Borror et al. 1989). Pheromones emitted by the hosts of ticks are kairomones because ticks are parasites, feeding from the blood of the host and possibly transmitting disease. A great deal of work on this topic has been conducted by John F. Carroll for the USDA at the Parasite Biology and Epidemiology lab, in Beltsville MD. Caroll has extensively studied the kairomones responses of
blacklegged ticks (*Ixodes scapularis*) to its primary host, white-tailed deer (*Odocoileus virginianus*).

In an earlier study, Carroll et al. (1996) found that blacklegged ticks responded to substances obtained from the hair of white-tailed deer. The substances were secreted from tarsal and interdigital glands on the legs of the deer. In field studies, glandular substances were applied to artificial host-seeking vantage points. The ticks responded more to a combination of the tarsal and interdigital gland substances than to either of the kairomones alone. Kairomonal response was supported by laboratory assays reported in the same paper. Glandular substances and nonglandular samples obtained from the foreheads and backs of deer were applied to glass tubes, which acted as questing vantage points. Female ticks displayed a greater response to the glandular substances than to the non-glandular samples (Carroll et al. 1996).

A few years later, Carroll (2001) reported that blacklegged tick responses to interdigital glands of the hind legs of deer are independent of tarsal gland responses. This study indicated that female-blacklegged ticks are attracted only to the interdigital gland substances, and that tarsal gland substances may actually contaminate interdigital gland substances. He was unable to determine the distance from which ticks can detect kairomones, but they climb up the stem of plants with glandular residues on the twigs. Carroll suggests future technology in which host kairomones are placed a few meters from human and deer trails so that ticks are attracted to sites without actual hosts, thus reducing the spread of disease (Carroll 2001). The urine of white-tailed deer has also been examined for its kairomonal qualities (Carroll 2000). Urine from does in and out of estrous, dominant and non-dominant bucks, and a combination of several types of urine
was tested at 95 and 50% relative humidity. It was found that at 50% relative humidity, ticks responded to the urine from does in estrous, dominant reproductive bucks, and the urine mixture. Carroll concluded that blacklegged deer ticks might use urine to select host-seeking sites under the proper humidity (2000).

Tick-host specificity response to kairomones has also been examined. In the laboratory, blacklegged tick (*Ixodes scapularis*), lone star tick (*Amblyomma americanum*), and American dog tick (*Dermacentor variabilis*) responses to kairomones from their respective primary hosts were compared to tick responses to alternate host kairomones (Carroll 2002). Blacklegged and lone star ticks exhibited arrestment behavior in response to dog kairomones and American dog ticks responded to deer kairomones in lab assays. Blacklegged and lone star ticks are often found on non-primary hosts. American dog ticks, however, are seldom found on alternate hosts, failing to explain the kairomonal response to deer substances. Without conducting a chemical analysis, Carroll was unsure if all potential hosts secrete a similar kairomone that all tick species respond more or less equally to, or if all hosts secrete different kairomones that different tick species choose to respond to (2002).

*Host-Seeking Behavior in Response to Host Species and Distribution*

Ixodid ticks exhibit different questing behavior depending upon several host factors. Ticks may change questing location, questing height, host attachment site, and even the type of host they attach to in response to host variables.

To determine if blacklegged and lone star ticks, which are primarily parasites of white-tailed deer, are more prevalent along deer trails, Shulze et al. (2001) measured tick densities for four years. Densities were measured in five different tick/deer habitats
along deer trails and along randomly selected, non-deer trail related transects. To ensure deer used the trails often, deer bait stations were placed along those trails. After four years of monitoring, no significant difference in tick density was found. The researchers speculate that factors such as microclimate conditions may affect tick location rather than host densities (Schulze et al. 2001).

In Japan, the bush tick (*Haemaphysalis longicornis*) has been shown to alter questing height depending upon the average body size of their hosts in that specific location (Tsunoda & Tatsuzawa 2003). Bush ticks feed primarily upon sika deer (*Cervus nippon*), of which physical size varies considerably between different locations in Japan. Field studies showed that questing height of the bush ticks was positively correlated to the body size of deer at that location. In one location, bush ticks were limited in questing height due to low vegetation height, but the same ticks in the lab were found to climb glass tubes to a height associated with the level of the hind legs of the deer. The authors believe that this questing height is a genetic factor adapted to the size of the hosts in the area (Tsunoda & Tatsuzawa 2003).

Feeding site on a host by a tick may vary with host species. The blacklegged tick, (*Ixodes scapularis*), differs in feeding location whether feeding on a white-tailed deer or a horse (Schmidtmann et al. 1998). When feeding upon deer, male and female ticks were primarily found on the outside of the ear, and on the head, neck, and chest, all of which are on the anterior portion of the animal. When located on horses, ticks were found feeding under the jawbone, chest, and in the axillary regions of both the fore and hind legs. Believing attachment site is related to sun exposure, the authors explain that the shorter hair of horses is why ticks were only found on the underside of those hosts. The
longer hair of white-tailed deer allows for attachment to more dorsal areas such as the head and neck, but does not explain attachment to the outside of the ears, though the authors speculate ticks may be picked up at this location during evening host-feeding when sun exposure is not an issue (Schmidtmann et al. 1998).

Various Ixodid ticks in Australia have been studied to determine how specific hosts must be (Belan & Bull 1995). Two generalist ticks, *Amblyomma limbatum* and *Aponomma hydrosauri*, which feed upon several snake and lizard species, were compared to two specialist ticks, *Aponomma fimbriatum* and *Tachyglossus aculeatus*. *A. fimbriatum* feeds on few species of snakes and lizards, while *T. aculeatus* feeds only on echidnas. Adults and larvae of the four tick species were exposed to a variety of known hosts, related hosts, and non-hosts for periods of 30 minutes. Successfulness of locating a potential host was determined by whether the tick contacted the skin of the host. Belan and Bull (1995) found that the adults of the generalist feeders located and attached to more host species than the adult specialist feeders. However, the larvae of all species were attracted to an equally wide range of potential hosts. The specialist larvae species soon detached from non-hosts, expressing the host-specificity of that species. The authors explain this intraspecific difference in host-seeking ability with two possibilities. The first is that adult ticks are able to properly identify suitable hosts because of prior experience. The other explanation is a possible morphological difference in sensory capacity between larvae and adults (Belan & Bull 1995).

**Climatic and Spatial Effects**

Questing behavior and host-seeking activity level of Ixodid ticks can vary due to several non-host related factors. Changes in temperature, relative humidity, and season
can alter tick activity. Of the greatest importance however, are changes in micrometeorological and microenvironmental components, to which ticks express a high degree of sensitivity.

In 1986, Harlan and Foster of Ohio State University found a positive correlation between host-seeking activity of American dog ticks and ambient temperature at 1900 hours (7:00 PM). No relationship was found between tick activity and relative humidity, insolation, average daily temperature, or ambient temperature from other times of night. Weather data was provided by the National Oceanic and Atmospheric Administration. The authors believe the temperature data from 1900 hours correlates to tick activity because of the feeding time of the ticks, from dusk to 2200 (Harlan & Foster 1986). This study did not examine any micrometeorological or microenvironmental factors.

Building upon their previous study, Harlan and Foster conducted another study concerning tick host-seeking activity (1990). In this paper, the authors examined the relationship between tick activity and fifteen micrometeorological or microenvironmental factors. Those factors included temperature and relative humidity 1m and 2.5cm above as well as within the litter layer, solar radiation 1m and 5cm above the litter layer, wind speed 1m and 15cm above the litter layer, soil temperature to a depth of 5cm, soil water content from the top 5cm, soil particle size, and vapor pressure deficits. Data was collected from five different sites with different cover types over a period of two weeks at the height of *Dermacentor variabilis* activity. Using regression models, Harlan and Foster found that ambient temperature at both 1m and 2.5cm above the leaf litter had the greatest effect on tick activity (determined by drag sampling). Local humidity and vapor pressure deficits were also important, but not to the extent of ambient temperature. Other
micrometeorological and microenvironmental factors had no significant bearing on tick host-seeking activity (Harlan & Foster 1990).

Using glass tubes as tick habitat in a laboratory study that manipulated temperature and relative humidity, Vail and Smith (2002) measured questing height, distance moved, and time spent in questing posture of blacklegged ticks. They found that ticks searched for hosts higher up in the glass tube at 100% relative humidity than at any other humidity and that the greatest distance moved and the greatest time spent in questing posture was at 25°C (Vail & Smith 2002).

Ticks are often sampled in an area to determine population abundance, giving an estimate of the potential risk of Lyme disease. Suspecting that sampling at different times of day may yield different results because of changing activity levels, Schulze and Jordan (2003) collected ticks at different times of day and differing levels of relative humidity. On the same day, using drag-sampling methods, *Ixodes scapularis* was more prevalent in samples collected in the morning. *Amblyomma americanum*, however, was collected in greater densities in the afternoon. The authors suggest that the different tick species are questing at different times of day in response to varying environmental conditions and that tick sampling needs to be standardized (Schulze & Jordan 2003). Unfortunately, their study doesn’t isolate whether it is time of day, humidity level, or temperature that affected tick species density.

Over the course of five years in the Bluegrass region of Kentucky, Burg (2001) studied the spatial and seasonal relationships of American dog ticks. Using random transects next to and away from host-trails, Burg found that ticks were not distributed randomly or uniformly. Instead, there were “hot-spots” of ticks in homogenous
microenvironments of suitable conditions. *D. variabilis* was sampled weekly using drag sampling from March until September to determine peak activity. The first peak activity period occurred from mid-April through late May. The second period was in July, and then all host-seeking activity ceased in August. Though Burg didn’t sample over winter, his results that tick activity ends in August differs from a study by Carroll and Kramer (2003). In this study, it was found that blacklegged ticks were active many days in January and February, even in conditions such as 70% snow cover and temperatures down to -2°C. Even though these two studies examined activity levels of two different tick species, more studies are needed to learn year-round host-seeking behavior.

**Conclusion**

The host-seeking, or questing behavior, of tick species can vary with several factors. The degree to which ticks respond to the kairomones of different species and even to the urine of different sexes of the same species differs. Questing height and attachment site may vary depending upon host characteristics, though host density may have little effect upon tick location. The ability to identify hosts can vary with tick maturity, an important factor to specialist parasites. Ambient temperature, relative humidity, season, and time of day can change tick host-seeking behavior, but not nearly as much as micrometeorological and microenvironmental effects can. Ticks are medically important parasites of vertebrates; because of this they have been the subjects of many experiments. There is a great deal known, but there is always more that can be learned about these organisms.
References


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