Vector Population Dynamics in Relation to Tick-Borne Arboviruses: A Review

Daniel E. Sonenshine

Department of Biology, Old Dominion University, Norfolk, Virginia 23508.

Part of the research reported in this paper was supported by Contract No. AT-(40-1)-3514 with the Division of Biology and Medicine, U.S. Atomic Energy Commission, Washington, D.C. The financial assistance of the Old Dominion University Research Foundation is gratefully acknowledged.

Introduction.—The Acari, or ticks and mites, are well known as pests and disease vectors affecting man, livestock, and wildlife. Species of ticks and mites transmit a remarkable variety of pathogenic organisms, probably more than any single order of insects. Included among these acarine-borne pathogens are protozoans, bacteria, rickettsiae, and numerous arboviruses. In addition, certain of the acarines are themselves directly responsible for death or injury to man or animals by inoculating toxins, paralytic agents, or inducing allergic responses, as well as exsanguination and general discomfort; e.g., "tick worry."

Arboviruses constitute perhaps the largest single group of pathogenic agents vectored by acarines, almost all by ticks. According to Horsfall and Tamm (13), this term is reserved for viruses which are biologically transmitted to susceptible vertebrate hosts by blood-sucking arthropods. These viruses multiply in both vector and host, but produce a pathogenic response and viremia only in the vertebrate host. Three main groups, (A, B, and C) each with many subgroups have been recognized by specialists for many years. A new group, the arenoviruses [which was discussed by Casals, et al. (4)], has been proposed to include certain antigenically related zoonotic viruses which do not require an arthropod for their transmission (e.g., Argentinian and Bolivian Hemorrhagic Fever, Lymphocytic Choriomeningitis, Lassa Fever, etc.). Since these latter agents are not necessarily vector borne, they will not be considered further here. Tick-borne viruses include at least 50 distinct entities (Tables 1 and 2) of more than 200 arboviruses known to date. Others are known which have not been reported in publication. According to Yunker (43), approximately 50 are known, most of which were described in the past decade. Few arboviruses are mite-borne. Consequently, we will focus our attention on the tick-borne viruses.

A brief review of tick-borne viruses.—Table 1 lists the tick-borne group B viruses. Most of these agents are manifested by an encephalitis syndrome in their vertebrate hosts similar to poliomyelitis. The most characteristic pattern is that observed with agents of the tick-borne encephalitis complex. In man, the Russian far eastern type may result in violent illness with high fever, nausea, vomiting, photophobia, and even coma or delirium. The bulbar centers of the brain and the cervical region of the spinal cord are characteristically involved, but ascending paralysis is often seen. In more benign cases, there may be only a serous meningitis, or the illness may occur in varying degrees of severity between the two extremes. The fatality rate is high, between 20-29%, while nonfatal cases frequently recover very slowly and are often left permanently paralyzed. The Central European type tends to be more benign, with lower mortality (13). Some of the Group B agents are primarily known from livestock, but may also infect man. Another important clinical syndrome induced by Group B viruses is hemorrhagic fever, typified by Omsk Hemorrhagic fever. In this case, the dominant symptoms are epistaxis, uterine and gastrointestinal bleeding, as well as signs of bleeding accompanied by headache and fever. The organism multiplies in the vascular system, in contrast the neurotropic growth seen in the encephalitides. However, Kysanur Forest Disease exhibits an intermediate clinical picture commonly with internal hemorrhaging, mild meningoencephalitis, as well as some of the other symptoms seen in both disease types. Most of the tick-borne Group B viruses are Palearctic or Oriental in distribution. Only one (Kadam virus) is known from the Ethiopian region; it is transmitted by the ticks which infest livestock. Another (Powassan encephalitis) is known from the New World, being originally described in Ontario, but now has been identified in New York State, Colorado, and South Dakota. Studies with small mammals also suggest its presence in British Columbia (43). All of these Group B agents are transmitted by ticks of the family Ixodidae.

Table 2 lists the remaining known tick-borne viral agents reported in the literature. Others are known, but have been excluded because they have not been proven to be tick-borne [e.g., an "apparently related" neurotropic virus from European roe deer, cited by Hoogstraal (8)], or have not been reported in publication. In addition, arboviruses primarily transmitted by insect vectors are excluded, even though there is evidence implicating tick transmission (8). Some of the ungrouped tick-borne viruses are known to produce clinical disease in man. Colorado Tick Fever (CTF), the most widespread and best known of the tick-borne virus diseases in North America, produces fever, headache, and retroorbital and muscle pains. However, encephalitis symptoms and severe bleeding are complications which may also occur. Clinical disease is most serious only in children. Other tick-borne viruses included here have produced encephalitis-like disease (i.e., Kemerovo, Tribec, and Uukuniemi), febrile symptoms (Quaranfil, Dugbe, Ganjam, Thogoto, Bhanja, and Nairobi Sheep Disease) or hemorrhagic fever symptoms (Crimean Hemorrhagic Fever) in man and animals. The latter symptoms have been the subject of extensive clinical epidemiological and acarological investigations, especially by Soviet workers. The clinical symptoms seen with Crimean HF (Central Asian and Uzbekistan HF) are similar to the previous description for Omsk Hemorrhagic Fever, but much more severe, in some regions reaching 30% mortality (13). This is perhaps the most widely distributed tick-borne

TABLE 1. A summary of arboviruses transmitted by ticks reported in recent literature. Group B viruses

Virus name	Reference[a]	Zoogeographic region	Dominant vector(s)	Hosts Overt	 Reservoir(s)
TBE Complex[b]	(13)				
1. (RSSE)[c]	(13)	Palearctic	*I. ricinus, persulcatus*	Man	S.M.[f]
2. (CEE)[d]	(13)	Palearctic	*I. ricinus*	Man	Birds, others
Kadam	(43)	Ethiopian	*R. pravus*	...	...
Kumlinge	(27, 43)	Palearctic	*I. ricinus*	Man	Livestock (?)
KFD[e]	(3)	Oriental	*Haemaphysalis* sp.	Man	Monkeys
Langot	(13)	Oriental	*I. granulatus*	Man (?)	Forest rats
Louping ill	(13)	Palearctic	*I. ricinus*	Man, Sheep	S.M., Birds, others
Negishi	(3)	Palearctic	Tick	Man	...
OHF[f]	(3)	Palearctic	*D. pictus* *I. apranophorus* others	...	...
Powassan	(3, 13)	Nearctic	*I. cookei* *Ixodes marxi*, others *D. andersoni*	...	...

[a] Reference in literature cited section of text. Refers to recent authorities on viral taxonomy.
[b] Tick-borne encephalitis.
[c] Russian Spring Summer Encephalitis.
[d] Central European Encephalitis.
[e] Kysanur Forest Disease.
[f] Omsk Hemorrhagis Fever.
[g] Small mammals.

virus-caused disease in man, and is known throughout much of the Soviet Union, Bulgaria, Pakistan, and across Africa from Kenya and Uganda to the Congo and Nigeria (4). In addition to the ungrouped viruses known to produce disease in man or domestic animals, are the remainder of those listed here which have unknown disease potential. These have been isolated primarily or exclusively from ticks. One of the most interesting is the Quaranfil group which, although known to have caused human illness in Egypt, has been reisolated repeatedly from *Argas* ticks in Egypt (8, 14, 15) and more recently in Afghanistan (42) without any association with human illness. Recently, an isolate similar to Quaranfil was made from *Ornithodoros capensis* Neumann ticks from Johnston Island in the Central Pacific. Thus, the range of these viruses, or at least viral groups, may be very great, a fact which suggests migratory bird transport. Hoogstraal, et al. (10, 11, 12) were among the first to demonstrate the importance of this means of disseminating infectious tick-borne agents; in this case between Europe, Asia, and Africa. Hoogstraal, et al. (11) noted that over 20 strains of pathogenic viruses were isolated from birds and their ticks examined in Egypt during only one fall migration period. L'vov, et al. (17) reported the isolation of 41 strains representing at least two arboviruses from *Ixodes uriae* White from a bird colony in the Sea of Okhotsk, and a virus indistinguishable from tick-borne encephalitis from this tick on another bird colony in the same area. Other viruses have been isolated from *O. capensis* in Trinidad (Soldado) and Australia. Hughes virus, which is highly pathogenic for suckling mice, has been isolated from *Ornithodoros denmarki* Kohls, Sonenshine and Clifford from Florida, Raza Island, Johnston Atoll, and the Farallon Islands (32). Presumably, this agent may be expected wherever its vector occurs. The importance of this migratory bird contribution was clearly described by Nuorteva and Hoogstraal (26) who noted that "hundreds of millions of migratory birds migrate for tremendous distances twice each year", spreading ticks infected with numerous pathogenic agents. Although these authors were concerned primarily with land birds, it is evident from the above discussion that sea birds also play an important role in spreading other pathogenic agents. In this case, the spread may be far greater than with land birds, as indicated by the immensely wide, virtually cosmomarine distribution of the sea bird ticks, *O. capensis*, or *I. uriae*, both of which have yielded viruses. The true epidemiological significance of the existence of these potentially dangerous pathogens carried in this exquisitely efficient distribution system has yet to be established. A summary of the geographic distribution of tick-borne viruses is illustrated in Fig. 1.

The preceding discussion described the rapid growth of knowledge concerning tick-borne viruses, most of which have been discovered within the last decade (43). However, I would be remiss in allowing this review to be considered as anything other than an appraisal of the state of knowledge based upon current literature. The several excellent recent reviews of this subject by Hoogstraal (8, 9) and Yunker (43) are rapidly becoming obsolete as a result of new isolations or recognitions of the identity of agents previously considered distinct. Nevertheless, the outstanding fact remains that the tick-borne viruses have now been shown to constitute a complex, highly varied assemblage of numerous pathogenic agents with implications of serious, and, indeed, ever-increasing public health importance. Consequently, it is pertinent to pause at this juncture to ask whether steps are being taken to obtain adequate knowledge of the ecology of the dominant vectors which would be the target species in any future control program.

The need for obtaining adequate knowledge of the ecology of the dominant vector ticks is magnified, to a considerable degree, by the biological characteristics of ticks which immensely enhance their efficiency as vectors. Ticks are remarkably long-lived. Many, if not most, have life cycles that extend over a period of years; certain *Ornithodoros* spp. may live for 25 yr when starved between molts (28). Many ticks survive long periods without feeding and still retain their pathogens; perhaps the longest documented is *Ornithodoros turicata* (Dugés) which survived 6 yr and 9 mo, and still transmitted spirochetes when allowed to feed. Digestion in ticks is primarily intracellular; hence virus particles need not be subjected to immediate enzymatic destruction. The hard ticks and the larvae of many of the soft ticks are slow feeders, facilitating extensive geographic dispersal by wide ranging hosts to which they are attached. Most of

TABLE 2. A summary of arboviruses transmitted by ticks reported in recent literature. Ungrouped viral agents

				Hosts	
Virus name	Reference[a]	Zoogeographic region	Dominant vector(s)	Overt	Reservoir(s)
Art-285	(42)	Palearctic	*A. reflexus*	...	Pigeons (?)
Bandia	(43)	Ethiopian	*O. sonrai*	...	...
Bhanja	(43)	Ethiopian Oriental	*H. intermedia* *B. decoloratus*	Man(?)	Livestock
Chenuda	(43)	Palearctic	*Argas* sp.	...	Wild Birds
CTF[b]	(13)	Nearctic	*D. andersoni*	Man	Small Mammals
CHF-Congo[c]	(4)	Palearctic Ethiopian	*H. marginatum* others	Man	Hares Livestock
C5581	(4)	Australasian	*Ornithodoros* sp.	...	Seabirds(?)
Dera Ghazi Khan	(4)	Oriental	*Hyalomma* sp.	...	...
Dugbe	(43)	Ethiopian	*A. variegatum*	...	Livestock
Ganjam	(43)	Ethiopian Oriental	*Haemaphysalis* sp.	Man	Goats
Grand Arbaud	(43)	Palearctic	*A. reflexus*	...	...
Hazara	(3)	Oriental	*Ixodes* sp.	...	...
Hughes	(1)	Neotropical	...	...	...
	(1)	Nearctic	*O. denmarki*	...	Sea Birds
Johnston Atoll	(6)	Central Pacific	*O. capensis*	...	Sea Birds(?)
Kaisodi	(3)	Oriental	*Haemaphysalis* sp.	...	...
Kemerova	(13)	Palearctic	*I. persulcatus*	Man	...
Lanjan	(3)	Oriental	*Dermacentor* sp.	...	...
Lipovnik	(3)	Palearctic	*Ixodes* sp.	...	...
Lone Star	(16)	Nearctic	*A. americanum*	...	...
Mono Lake	(3)	Nearctic	*Argas* sp.	...	...
Mutucare	(3)	Neotropical	*Ornithodoros* sp.	...	...
NSD[d]	(13)	Ethiopian	*Rhipicephalus* sp. *Amblyomma* sp.	Man	Sheep
Nyamanini	(14)	Palearctic	*Argas* sp.	...	Wild Birds
Pak Argas 461	(3)	Oriental	*A. reflexus*	...	Pigeons(?)
Pak Argas 487	(3)	Oriental	*A. reflexus*	...	Pigeons(?)
Ponteves	(43)	Palearctic	*A. reflexus*	...	...
Qalyub	(39)	Palearctic	*Q. erraticus*	...	...
Quaranfil	(14, 15)	Palearctic	*A. arboreus*	Man	Small Mammals Wild Birds
Sawgrass		Nearctic	*D. variabilis* *H. leporispalustris*	... ...	... ...
Silverwater	(3)	Nearctic	*H. leporispalustris*	...	...
Soldado	(43)	Neotropical	*O. capensis*	...	Sea Birds
SMCA[e]	(5)	Nearctic	*Haemaphysalis* sp.	...	...
Thogoto	(3)	Ethiopian	*B. decoloratus*	...	Livestock
Tribec	(43)	Palearctic	*I. ricinus*	Man	...
URB-TM 1381	(3)	Nearctic	*Amblyomma* sp.	...	...
Uukuniemi	(27)	Palearctic	*I. ricinus*	...	Livestock
Wad Medani	(3)	Palearctic	*O. erratius*	...	Small Mammals
Wanowrie	(3)	Oriental	*Hyalomma* sp.	...	...
Tyuleniy 1	(17)	...	*I. uriae*	...	Sea Birds
(unnamed) 2		Palearctic	*I. uriae*	...	Sea Birds

[a] References in text. Refers, in most cases, to recent authorities on viral taxonomy.
[b] Colorado Tick Fever.
[c] Crimean Hemorrhagic Fever (Central Asian Hemorrhagic Fever and Uzbekistan Hemorrhagic Fever).
[d] Nairobi Sheep Disease.
[e] Suckling Mouse Cataract Agent.

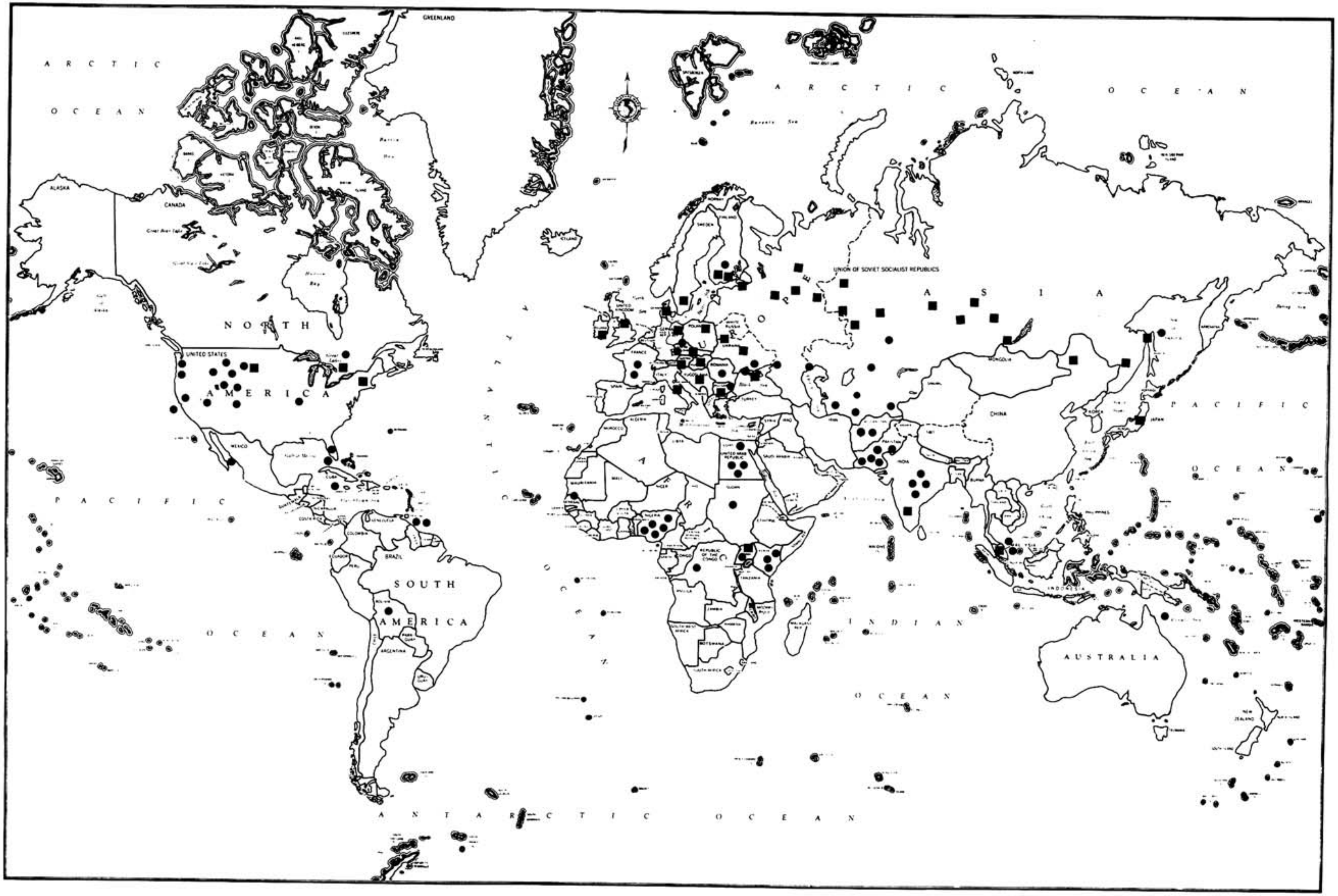


Fig. 1. Approximate geographic distribution of tick-borne arboviruses throughout the world. Each symbol represents where each distinct virus has been reported. Black squares represent Group B viruses; black circles, ungrouped viruses.

the tick species have efficient mechanisms for restricting water loss. Some are capable of direct sorption of atmospheric moisture. Most of the argasid ticks, as well as certain ixodid species, are well adapted to nest parasitism, surviving in ground burrows, caves, under rocks, in tree nests, and even man-made shelters. Many of the ixodid ticks that live by ambush parasitism enter diapause during periods of unfavorable climatic conditions which provides an additional mechanism for long-term survival of infectious organisms in the disease vector. The high vector potential of ticks is further compounded, and the public health or veterinary problem further complicated because most of the tick-borne pathogens circulate primarily in enzootic or epizootic cycles and often involve a variety of vertebrate host species.

These many disease-favoring attributes of ticks increase the need to understand the ecology of those species which are of known or potentially great public health and veterinary importance. Specifically, we need to understand the dynamics of the vector populations in the high-risk parts of their range to facilitate predictions concern the risk and spread of tick-borne disease.

Techniques for measuring vector population dynamics.—Study of vector population dynamics has been done by a variety of methods which are dependent upon behavior of the ticks and their hosts. Ticks have been captured by flagging, blanket dragging, CO_2 attractants, direct collection from nest sites, and from animal hosts, including sentinel animals. In some cases, the studies have been amplified by marking the ticks with paint, dusts, and radioisotopes to study population size, survival, or dispersal. A brief review of the techniques used in measuring important biodynamic phenomena by workers on tick vectors of disease is pertinent at this point to evaluate their contributions.

Flagging.—This is perhaps the most widely used technique for measuring tick numbers as well as for routine collections of ticks which find hosts by the ambush methods [Type III of Camin, (2)]. The flag, typically a large piece of cloth weighted on one side and affixed to a wooden pole, is swept across vegetation and may pick up ticks in an active ("questing"), host-seeking state of activity. Among the more important advantages of this technique are that (i) the area sampled is known, and (ii) the length of time the area was sampled is also known. Important disadvantages of the technique are that it collects only those individuals that are physiologically in a host-seeking state of activity, and only those individuals positioned so as to come in contact with the cloth. These latter objections can be alleviated in part by repeated sampling of the same area, but difficulties persist in relation to the density of the vegetation and physical obstructions. Other difficulties arise in relation to weather conditions; it is frequently unclear whether ticks are less active during wet weather or whether they are merely unable to cling to the wet cloth flag used to collect them.

Dragging.—Blanket drags are useful where sampling is done over large areas of open land with low, meadow-like vegetation (20, 23). The blanket is dragged across the pasture or other open area by one or two workers and covers a much larger area than a hand-held flag. The technique offers the same benefits and suffers from the same disadvantages as are found with flagging, though in lesser degree since the limitation for more uniform vegetation also reduces the degree of error.

Attractants.—Garcia (7) reported on the use of CO_2 ("dry ice") as an attractant for ticks. He noted that the ticks moved along a concn gradient towards the release point. The method has been appliedby Clark, et al. (5) for research on the ecology of Colorado Tick Fever in mountainous areas in western Montana. The method is especially beneficial as a convenient means of trapping ticks in the immediate area affected by the gas, and is especially useful on very rough, steep talus slopes where flagging is impractical. Unfortunately, the technique suffers from several disadvantages which hinder interpretation of the capture results, especially (i) that the size of the area sampled is not known precisely, and (ii) that the proportion of the population which respond to the attractant under field conditions is unknown.

Host examination.—Direct examination of animal hosts provides a means of monitoring relative tick abundance when the ticks cannot be obtained by direct sampling. When direct sampling is feasible, host examination is useful for determining the proportion of the active population which find hosts. Thorough examination is tedious, and it is often difficult to insure complete removal or to obtain exact counts of all ticks present, especially if the field plan involves live processing of the hosts. However, meaningful seasonal activity data can be obtained by this means.

Collections from nest sites.—Direct collection is often made from nest sites, such as burrow sand, nesting material, cracks in walls of buildings, under rocks near nests, and so on. Such collecting is usually done to gather ticks for laboratory study. However, the small size of the site and the limitations on tick dispersal enhance the opportunities for direct study of population dynamics of nidiculous ticks. It is surprising that few population studies have in fact been done on such ticks, even though almost all of the argasid and many of the ixodid ticks are nidicoles. One of the interesting recent studies (Galun, Avivi, and Warburg, *personal communication*) "involved determination of populations of *Ornithodoros tholozani* (Laboulbene and Meguin) in caves in Israel". Studies were done on more than 100 caves. Soil samples of uniform size were removed and all ticks in each sample were counted, in order to ascertain which caves harbored tick populations. Subsequently, field-collected ticks were marked with various dyes and released in the same caves where they were captured. Estimates of the populations in four caves ranged from 1,100 to 16,225. These data were useful for attempts at population control by the sterile male technique.

Marking.—Various workers have marked ticks to study dispersal or to estimate populations. Smith et al. (35) measured dispersal and survival of *Dermacentor variabilis* (Say) by marking unfed adults with enamel paint and releasing them. To determine the extent to which engorged females would disperse in search (presumably) of suitable nesting sites, pieces of thread were attached to each tick. Sonenshine and Clark (38) and Sonenshine (*unpublished*) tagged large numbers of tick larvae of several species with ^{14}C and released them into defined study areas of known size. Some of the tagged ticks were recaptured by live capture of animal hosts in the areas. The recapture of these tagged ticks simultaneously with native, unmarked ticks provided a basis for determining many ecological attributes of the tick populations which could not be studied by any other means.

Review of studies on population dynamics of specific tick vectors of disease.—Several workers have contributed to our knowledge of this important ecological subject, in relation to diseases of local importance which their subject vectors transmit. This review will concentrate in depth on several of these studies in order to evaluate this knowledge and determine future needs. Specifically, the work on the ecology of *Ixodes ricinus* in relation to tick-borne encephalitis, on *D. andersoni* in relation to Colorado Tick Fever and on *D. variabilis* as an example of methods will be examined in depth.

—1) *Ixodes ricinus* (L.) and louping ill.—This tick has been the subject of more extensive ecological investigations than any other single species, no doubt because of its immense importance as a vector of several serious diseases of man and livestock. In the British Isles, this species has been the subject of extensive study in relation to the transmission of louping ill (LI) virus. The classical studies of Milne (20, 21, 22, 23, 24, 25) have contributed greatly to our understanding of the ecology of this tick-pathogen cycle in situations involving pasture and livestock. Milne (23) working at a sheep farm in hilly country in northern England, noted that sheep feed in valleys and lower slopes during the day but rest on the heights at night. They utilize well defined paths for these movements. Pairs of blanket drags were made in this area. Each consisted of a 50-yard drag along the path and a parallel drag 6-10 yards in the adjacent pasture. It was found that sheep paths were no more intensely infested than the adjacent pasture. In addition, only 4% of the total was found on the "night lairs", i.e., the hill tops where the sheep rest (23). Milne noted that the hill top vegetation consisted of fine short grass or herbs on dry ground with little or no underlying mat, in contrast to the long, rough grasses and extensive mat found in the valley pastures. Altitudinal variations were dismissed as of no importance except as it influences the character of the vegetation. To measure population, three uniform sections of pasture of equal size (characterized by a more or less uniform plant species composition, density, and thickness) were sampled repeatedly. Blanket dragging was done throughout the tick season and all ticks captured were destroyed. This program of "exhaustion" sampling comes as close as is practical to a direct sampling method (23). Tick populations were not uniform, but it was felt that since the differences were small, uniform distribution of ticks might be expected when larger areas were compared. The total numbers taken in a plot were believed to reasonably reflect the actual total population present. Presumably, then, the entire population in the entire area of comparable vegetative cover could be estimated by expansion of the sample numbers. Milne (23) estimated that a very heavily infested pasture supported approximately 20 unfed females and 100 unfed nymphs/100 sq yards during an entire activity season. However, other data obtained by single blanket drags of virgin sites only (i.e., never previously dragged) did not support the hypothesis of uniform density. An important factor influencing the study was the limited labor available relative to the size of the sampling areas required for an adequate sample.

In other papers (24), Milne showed that most of the very large number of wild bird and mammal species reported as hosts for *I. ricinus* contribute only slightly to its maintenance. Perhaps the most important wild species were the Scottish mountain hare *Lepus timidus* (L.) and the red deer, *Cervus elaphus* (L.); the latter may carry several times as many ticks as do sheep, but are present in much smaller numbers. Milne estimated the relative contributions of different host animals selected in relation to size classes for female *I. ricinus*, to be, approximately: red deer, 500; sheep, 150; brown hare, 10; rabbit, less than 1; and "mouse", 0. Similar, though higher values were said to hold for nymphs and larvae. He then prepared a ranking of hosts based on the "sheep equivalent" and using actual collection data from wild animals (see Table 3). Red deer were omitted because none was captured and examined. It is noteworthy that with the exception of the red deer, all of the wild hosts rank far below the domestic sheep as tick hosts. Of course, the number of individuals of each contributory species in an area must also be considered in evaluating them as hosts. Milne did this for the wild fauna, integrating the mean population density with the mean number of attached ticks so as to arrive at a ranking, in terms of sheep equivalents, for 13 host species (Table 3). It is noteworthy that only 1%, approximately, of the total female tick population was estimated to be maintained by all of these wild species on "typical" northern England hill sheep farms. Sheep equivalents of different wild animals for nymphs were also calculated on the basis of their relative population density, in the same manner as for female ticks (Table 3). Some animals are omitted which may be important, notably the short-tailed vole. This animal, with a sheep equivalent for nymphs of only 0.0013 on an individual host basis, is nevertheless very abundant and 10-50 voles/acre may be expected even on rough grass grazings (24). Hence, its true contribution may be substantial, especially during periods of high vole density. In Central Europe, mice and other small mammals are known to be important as hosts for *I. ricinus*. In summary, in northern England hill pastures, sheep host 94-99% of the adult female *I. ricinus* and the great majority of the nymphs (24).

This brief review is not the place to attempt to describe the many excellent studies which have elucidated the seasonal activity patterns, microhabitat requirements, behavior and other important ecological attributes of *I. ricinus*. Mention should be made, however, of tick distribution in relation to biotypes. This is determined by the tick's requirement of near-saturated air and temperatures above 15 C long enough to support development (19). A thorough, excellent comparison of the tick support potential of contrasting vegetative cover types in Britain was given by Macleod (19). In Ireland, the tick has become established on well-grazed, low altitude pasture lands considered unsuitable for infestation in Britain, probably because of the more or less uniformly

TABLE 3. Relative ranking of wild hosts of the sheep tick, *Ixodes ricinus*, in northern England. Sheep equivalents for female and nymphal ticks

Avg individual wild host		Avg wild host population[b]		Avg wild host population[b]	
Host	Sheep equiv. for females	Host	Sheep equiv. for females	Host	Sheep equiv. for nymphs
Roe deer	0.1396	Hedgehog	1.62	Red grouse	10.66
Hedgehog	0.1353	Brown hare	1.54	Rabbit	6.16
Brown Hare	0.0771	Rabbit	0.97	Hedgehog	5.89
Stoat	0.0547	Stoat	0.87	Pheasant	3.51
Badger	0.0544	Pheasant	0.85	Skylark	1.19
Otter	0.0324	Red grouse	0.55	Meadow pipit	1.02
Fox	0.0233	Roe deer	0.42	Brown hare	0.96
Pheasant	0.0202	Badger	0.11	Weasel	0.36
Red grouse	0.0017	Fox	0.09	Wheateater	0.32
Magpie	0.0015	Otter	0.06	Partridge	0.19
Rabbit	0.0014	Magpie	0.01	Roe deer	0.13
				Stoat	0.12
				Lapwing	0.10
				Fox	0.06
				Long-eared owl	0.03
				Magpie	0.01

[a] Based upon data of A. Milne, 24). The ecology of the sheep tick, *Ixodes ricinus* L. Host relationships of the tick. Parasitology 39:173-197.

[b] Computed as a function of the avg individual sheep equivalent multiplied by the mean population density in the hill farms under study.

high rainfall and high atmospheric humidity prevalent in much of Ireland (40). Walton noted that cattle exhibited a marked preference for grazing on short grass pasture (76.4% of grazing time), limited interest in pasture dominated by rushes (14.8%), and little grazing elsewhere. Consequently, one would expect the highest tick densities in the short grass pasture. However, tick density (based on larvae) was found to be uniform with respect to four contrasting vegetative types sampled. Walton concluded that this result may be used to determine survival rates of ticks in each of the contrasting vegetative cover types sampled.

The epizootiology of louping ill involves a complex ecosystem in which small mammals (34) and other wildlife maintain the virus in nature, while "sheep and cattle act as amplifiers, increasing both the tick population and the incidence of LI infection" (41). However, studies described above have contributed the knowledge necessary to identify and quantitate the key elements in the pathogen ecosystem which involves the animals of primary interest, namely, the domestic stock. Knowledge of both the natural and post-vaccination incidence of LI infection in sheep and the probable incidence of tick infection was summarized by Smith (33). Consequently, it is possible to apply all of these elements in our knowledge to predict the probable risk of louping ill virus infection in livestock.

—2) Tick-borne encephalitis in central Europe.—Investigations on the ecology of tick-borne encephalitis (spring summer meningoencephalitis) in lower Austria were done in a natural focus in forested hilly country, (18, 29, 30, 31). These workers are among the first to attempt to obtain a comprehensive picture of the ecology of a tick-borne disease by simultaneous study of vector tick and host population dynamics, climatic conditions, vegetation, and the incidence of infection in a single natural focus over an extended period of time. Two small study areas, each 3,600 m^2, were established in the hillside focus representing a total area of approximately 6 hectares (ha). These study areas included three vegetative cover types; (i) mature evergreen forest with little underbrush, (ii) "young" mixed forest regeneration with a heavy understory of underbrush, and (iii) meadow-forest margin. Ticks, including all active stages of *I. ricinus*, were collected directly by dragging at systematically positioned sampling points, each 16 m^2, distributed throughout each study area and representing approximately 0.5 to 1.0% of the total area of the focus. Live trapping was done to collect small mammals. More than 35,000 ticks and numerous small mammals were processed for virus isolations.

Table 4 summarizes the estimates of the total numbers of *I. ricinus* in a uniformly comparable sampling area, and, based upon that, in the entire study area. These estimates from Loew, et al. (18) are themselves based on more extensive data, but only data for comparable collecting periods were used. Great variations appear to have occurred in the density of larvae and adults, but not of nymphs, between 1961 and the later years. Tick densities in relation to three of the more important vegetative cover types in the focus are summarized in Table 5, also based on Loew, et al. (18). The forest-meadow ecotone was clearly most important for nymphs and adults in all 3 yr. The young second growth forest also supported large numbers of nymphal and adult ticks, while the mature, old evergreen stand was least important for support of ticks. Larval densities varied so greatly between vegetative types in different years that the role of these cover types for larval support is much less clear. However, in this case also, the old mature forest supported the lowest numbers of ticks.

Small mammals appear to represent the dominant

TABLE 4. Estimated populations of developmental stages of *Ixodes ricinus* L. in a focus of tick-borne encephalitis in Austria[a]

	Larvae		Nymphs		Adults	
Year	Sample points (256 m^2)	Total focus (60,000 m^2)	Sample points (256 m^2)	Total focus (60,000 m^2)	Sample points (256 m^2)	Total focus (60,000 m^2)
1961	7,117	1,668,047	1,213	284,327	36	8,440
1962	2,534	593,970	1,571	368,242	175	41,020
1963	3,604	844,778	2,897	679,057	157	36,800
Mean	4,418	1,035,598	1,894	443,875	123	28,753

[a] Based upon data from Table 5 of Loew, et al., (18), and expanded to entire area of the focus (60,000 m^2); based on collections done at 16 control points (16 m^2 each) at the same time periods during the 3-yr period, 1961-1963.

TABLE 5. Comparison of relative density of developmental stages of *Ixodes ricinus* per sample site (16 m^2) in three contrasting vegetative cover types in a tick-borne encephalitis focus in Austria[a]

		Biotype 1	Biotype 2	Biotype 3
Developmental stage		Mature evergreen forest	Meadow-forest margin	Young forest regeneration
Larvae	1961	19.0	14.7	80.4
	1962	8.6	3.6	25.1
	1963	6.6	19.9	16.2
Mean		11.4	12.7	40.6
Nymphs	1961	6.8	34.0	20.0
	1962	3.9	39.8	18.3
	1963	4.8	33.8	19.1
Mean		5.2	35.9	19.1
Adults	1961	0.3	1.9	0.9
	1962	0.2	7.4	2.1
	1963	0.2	2.2	0.9
Mean		0.2	3.8	1.3

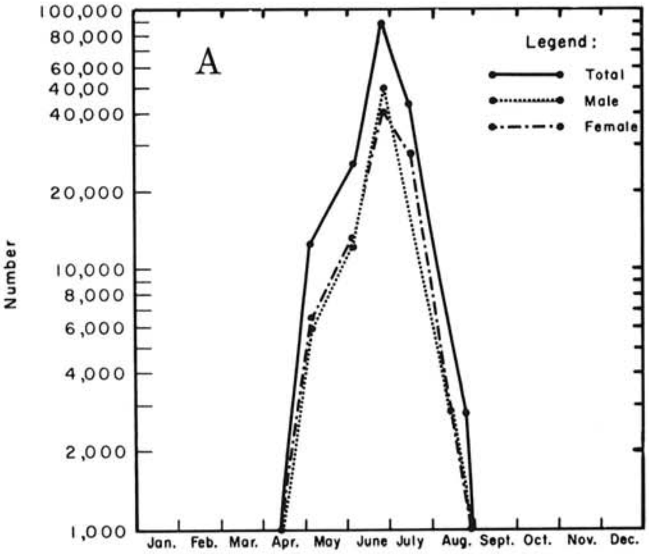
[a] Data from Table 6 of Loew, et al. (18).

hosts for maintenance of the immature stages of the vector in this focus, while larger mammals, especially deer, are thought to support the adults. Data summarized by Pretzmann, et al. (30) and Loew, et al. (18) indicates that approximately 700 small mammals were present in the focus in 1962 [in a later paper, (30)], the estimated number given is 40/ha, or 240 for the entire focus); 258 were believed present in 1963. These animals comprised four species, *Apodemus flavicollis* Wintoni, *A. sylvaticus* (L.) *Clethrionomys glareolus* Schreber, and *Microtus arvalis* Pallas. Host examinations revealed a mean incidence of infestation of 17.5 larvae/animal for the period May through October. To calculate the total tick support potential of the host population, the authors used these data and the estimated mean duration of feeding [approximately 4 days according to Pretzmann, et al., (29)] to arrive at an estimated 31,920 engorged larvae in the study area in 1962 (or 560,000 in the entire 6-ha focus). Similar calculations were used to estimate the numbers of engorging nymphs, approximately 915 in the study area (or 15,250 in the entire focus). The values for engorging larvae are larger than for unfed nymphs, which suggests that small mammals host almost all of these ticks. However, such is not the case for nymphs; the total number of nymphs engorging on small mammals was less than half the number of unfed adults present in the focus. Consequently, the authors conclude that other mammals, especially hares and deer contribute substantially to support of these ticks.

Data on virus infections in ticks and in small mammals were used in conjunction with the ecological data described above to quantitate the virus cycle in the natural focus. It is evident that a primary cycle exists involving the vector, *I. ricinus*, and small mammals. These animals become infected primarily as a result of infestation with infected larvae. Using serological data on the incidence of virus infection (5%) in mice, population density of mice, and the estimated yield of fed ticks, the authors predicted the presence in the focus of an annual average of seven viremic mice, 400 infected engorged larvae, and 200 (assumed molting mortality) infected flat nymphs per ha.

The value of these studies, perhaps, lies more in the comprehensive picture of the biocenose in which the tick-borne encephalitis virus circulates than in the validity of the estimates of tick numbers, host density, or virus infection. The quantitative aspect of this knowledge facilitates ranking of host species, vegetative cover types and other important ecological parameters. Consequently, such studies provide a detailed, quantitative picture of the elements essential for successful virus propagation in the natural environment.

—3) Colorado tick fever.—This is the best known and perhaps the most important of the tick-borne virus diseases in North America. Human cases have been reported mostly from the Rocky Mountain and western most areas of the U.S. The natural cycle involves small mammals, especially ground squirrels and immature wood ticks, *D. andersoni*. Studies by Clark, et al. (5) in a Colorado tick fever (CTF) focus in a mountain canyon in western Montana revealed that virus could be readily isolated from immature wood ticks, in 15% to 35% of the tick pools tested in 1964 and 1966, respectively. CTF seropositive small mammal hosts were also detected; 3.5% and 5.9% in 1964 and 1966, respectively. The CO_2 attractant technique was used to determine relative adult tick density in contrasting habitats. Most were concentrated in the alpine meadows; few were found in the talus slopes or valley floor of the canyon focus. Marking was done to determine persistence of the ticks in the focus after they have become active. Rapid dispersal of the virus was believed to be accomplished by wide ranging small mammals.



Population Indices of Total Number of Adult *D. variabilis* by Mark and Recapture Montpelier Study Area, 1963-64

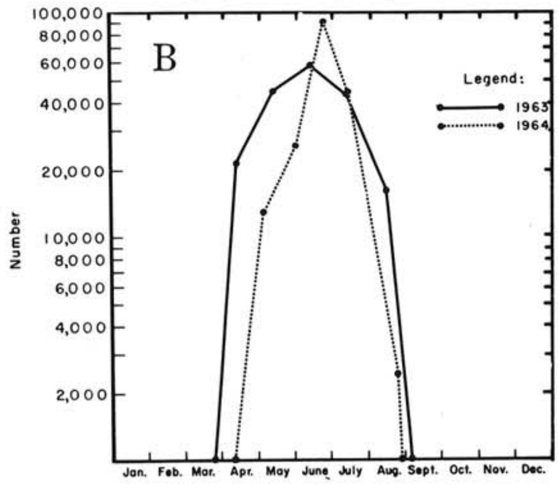


Fig. 2-(A, B). Estimated population of adult American dog ticks, *Dermacentor variabilis* based on mark-and-recapture tick flag collections in a 161.9-m^2 (40-acre) study area near Montpelier, Virginia. **A)** Monthly population indices for 1963. **B)** Comparison of monthly population indices of adult ticks in the same 161.9-m^2 area for 2 yr, 1963 and 1964. From Sonenshine, et al. (37).

To determine the population density of *D. andersoni* larvae in the CTF focus, Sonenshine and Clark (38) released 22,800 radioisotope-tagged larvae, in approximately equal numbers at each of numerous release points distributed throughout the study area. However, only a single trapping collection was made afterwards, and the recapture data for small mammals, though abundant, did not lend itself to estimating population size. Recently, Clifford, Yunker, and Sonenshine (*unpublished*) have continued these release-and-recapture studies. In 1967, 30,600 tagged larvae were released and 22 were recaptured in subsequent collections. These were found among 1,168 immature *D. andersoni* from 55 small mammals. The estimated population density of larvae in the focus in late July was 171,889 larvae/acre. Releases of tagged ticks were also made in 1968 and 1969 in a new canyon focus, but recaptures were too few to permit population estimates.

—4) Population dynamics of the American dog tick (*D. variabilis*).—Review of the ecological work done on this tick is pertinent to this discussion even though it has not been incriminated in the transmission of any important viral diseases of man or domestic animals. Studies by Smith, et al. (35) established the seasonal dynamics, major host relationships, dispersal and other ecological attributes of this tick. Recently, Sonenshine, et al. (37) studied the population dynamics of the dog tick in a study area comprising old fields and woodland in a rural region of Virginia. These workers established a uniform size tick sampling location (0.001 acre) in each of the 0.1 acre small mammal trapping plots distributed in the 60-acre study area. Ticks were collected by flagging each of the 600 sampling locations, marked and released where they were captured. Flagging but not marking was repeated within a few days and the proportion of marked and unmarked individuals was compared to estimate the tick population within the sampling area. The cycles of collecting, marking, releasing, and recapture were repeated throughout the tick activity season. The results were believed to be representative of the entire study area, since the sampling sites were located at random within each plot of the systematically placed trapping grids. Consequently, the population estimates were expanded to give the total population within the study area (Fig. 2). These studies, carried out during a 3-yr period, revealed that substantial differences in the total adult tick population size could be expected in different years; the estimated total adult tick population at peak density was 89,000 in 1964, but only 56,000 in 1963. Similar data for 1963 (not shown in the figure) indicated a peak population of 45,000. The total number of adults actively seeking hosts varied almost daily, especially in relation to changes in solar radiation, but never approached the total estimated abundance. This may have been due, in part, to the relative inefficiency of the flagging technique (maximum of 8%). But it also suggests that only a part of the adult population is in an active, host-seeking phase at any given time. The mark-and-recapture studies also revealed that dispersal of unfed ticks was very limited, with 93.1% subject to recapture at the original capture site, that overwinter survival of unfed ticks was rare (less than 5%), and that most adults were concentrated in the dense, low woody deciduous forest regeneration and adjacent old fields.

The results obtained by Sonenshine, et al. (37) with larvae and nymphs were less satisfactory because these ticks could not be captured by direct sampling methods. Examination of small mammal hosts was done to determine the relative importance of each mammal species in supporting the tick (Table 6). These results show that only two of the ten species examined in this area were important as tick hosts, namely, the meadow vole, *Microtus pennsylvanicus* (Ord) and the white footed mouse, *Peromyscus leucopus* (Rafinesque). This knowledge is important to an understanding of the epidemiology of diseases transmitted by this tick, since these hosts occur in habitats likely to be frequented by man, namely, old fields, and adjacent young forest regeneration.

To determine the total larval tick population, Sonenshine and Clark (38) and Sonenshine (36) reared large numbers of radioisotope-tagged larvae by inoculation of radiochemicals into engorged females just prior to egg laying. Suitably tagged larvae were obtained by radioassay of the progeny of these females. Field trials done with these ticks revealed that they could be recaptured in large numbers on wild rodents following their release. At first, many more tagged larvae than mature larvae were collected, perhaps because they were reared under the much lower light intensities of the laboratory and, therefore, were initially more responsive to the intense energy of summer sunshine than the wild larvae. However, it was also found that they would emerge in the following spring. Consequently, releasing of tagged ticks was planned for mid-summer, when the first indications of hatching of egg masses in the natural environment occur, to be followed by trapping to recover these ticks during the same season and the following spring. Approximately 250,000 tagged *D. variabilis* larvae were released each August during 1967-1969 at numerous predetermined sites in the same natural area where trapping was done. In addition, other samples were held in the natural environment in sealed cloth containers with soil and leaf litter to determine survival.

The data obtained by release and recapture of tagged ticks on wild hosts were used to estimate larval tick populations by the Lincoln index formula. In August, immediately after release, the estimated mean number of larvae/acre ranged from 491 to 1,256 (data for three yr). These values are based on the assumption of 100% survival of the tagged ticks. The true survival value is unknown, but survival tests done under natural conditions suggest that it is very high initially. In subsequent trapping collections, the mean number of larvae/acre tended to decline, so that only 65-75% of the larval numbers observed in August were observed in October. In contrast to the numbers present in late summer and fall, the values for mid-April ranged from approximately 29,600 to 48,300 larvae/acre. Consequently, the numbers present in late summer and fall must represent only a small proportion of the total larval tick population present, specifically those which were stimulated to seek hosts instead of entering diapause. These host-seeking individuals represent only 1-9% of the total number estimated to be present. This is in agreement with earlier results obtained by Sonenshine, et al. (37) who noted that larval host-seeking activity at this seasonal period was erratic, without a clearly marked peak, and at a much lower level than in the spring. Clearly, the vast majority of the larvae enter diapause without seeking hosts. The numbers present in spring are those which survived the winter and emerged from diapause at this time to seek hosts. The spring activity peak occurs in April, and the values given for this month probably reflect the true totals more closely than at any other time. After April, the estimated total numbers of host-seeking larvae decline, probably due to mortality or successful feeding.

TABLE 6. Frequency of occurrence of *Dermacentor variabilis* larvae and nymphs on small mammals. Summary tabulation for (60-acre) Montpelier study area 1963-1965[a]

Host species	Animal examinations: Total animal exam.	Animal examinations: Percent of all hosts	Tick occurrence: Larvae: Total no.	Tick occurrence: Larvae: Percent of total	Tick occurrence: Nymphs: Total no.	Tick occurrence: Nymphs: Percent of total
White-footed mouse	1,370	65.8	3,362	74.2	200	52.0
Flying squirrel	74	3.6	7	0.2	1	0.3
Ground squirrel	27	1.3	1	0.0	1	0.3
Pine vole	37	1.8	49	1.1	4	1.0
Meadow vole	316	15.2	1,060	23.4	176	45.7
Harvest mouse	175	8.4	49	1.1	2	0.5
House mouse	21	1.0	2	0.0	1	0.3
Shrews (3 species)	63	3.0	0	0.0	0	0.0
Totals	2,083	...	4,530	...	385	...

[a]Data from Sonenshine, et al. (37).

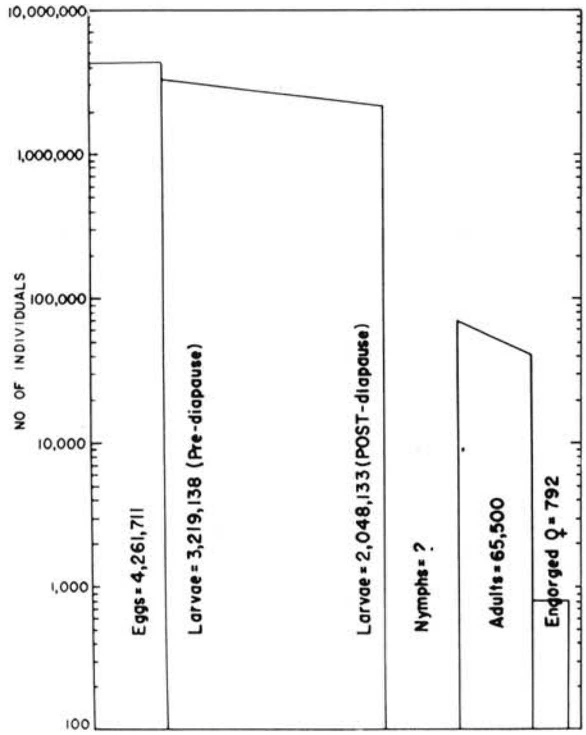


Fig. 3. Hypothetical model of a wild *Dermacentor variabilis* population in a 175.2-m^2 (43.3-acre) study area near Montpelier, Virginia, 1967-1968. Certain of the data used in construction of this model were obtained by mark-and-recapture (of radioisotope-tagged and otherwise marked ticks) techniques; other data, from laboratory studies on fertility, fecundity, and survival of these ticks. From Sonenshine (36).

Data on the total numbers of adults present in the study area was obtained by direct sampling and mark-and-recapture techniques. At the time of peak density, approximately 1,100 to 1,500 unfed adults/acre were estimated to be present. *D. variabilis* nymphs, though found on some of the animals examined, were not taken in sufficient numbers to permit estimates of population size.

Population estimates of the type described here include several of the essential elements needed to construct a life model of the tick population in the study area. Other elements (e.g., egg production and percent hatching) were obtained from laboratory studies in which field conditions were simulated (36). An example of this type of life model is shown in Fig. 3 for the period 1967-1968. The value of such a model of a vector population is that it provides a relatively simple (and, admittedly, oversimplified) picture of population structure' on a quantitative basis. The model can be refined as new data, e.g., on molting under natural conditions, becomes available. Deterministic equations can be developed with models of this type, so as to facilitate predictions of any of the quantitative values in the model in future years, or, in other regions within the range of the vector. Finally, it facilitates predictions of the risk of infection for man, once the percentage of infected vector individuals becomes known.

Future needs.—To conclude this review, it also may be pertinent at this point to consider the future. Knowledge of the occurrence of pathogenic organisms, especially arboviruses, in ticks has grown rapidly, and may be expected to increase, perhaps even more rapidly. However, knowledge of the frequency of infection in ticks and wild hosts has not kept pace with the findings on pathogens. Few studies have been done on population dynamics. Consequently, the risk to man or livestock posed by many of these agents cannot be assessed properly. In the case of Colorado Tick Fever, comprehensive study of the population dynamics of the wood tick in a typical focus would contribute substantially to the usefulness of data already accumulated on the ecology of the virus in the vector and in wild hosts. Nest-inhabiting ticks, such as the bird parasite, *O. capensis*, are also probably candidates for future population studies, not only because of the need to ascertain the total population potentially capable of infecting birds, but, also, to predict overwinter survival of virus in tick-infested nests and the degree of virus dispersal possible by bird transport of infected ticks. Population studies on the vectors of Crimean Hemorrhagic Fever, done in conjunction with examination of migratory birds for ticks and virus infection, would appear to be a needed study. Such a study would determine the proportion of the infected vector population transported by migratory birds, the dispersal range, and, consequently, the potential geographic location of new foci. Finally, additional studies on the population dynamics of vectors such as *I. ricinus* or *D. variabilis* need to be done in different parts of their range so as to determine the extent to which different biocenoses, with different vegetative cover types, host spectrum, and climatic factors affect the vector population and the incidence of infection.

LITERATURE CITED

1. AITKEN, T. H. G., A. H. JONKERS, E. S. TIKASINGH, and C. B. WORTH. 1968. Hughes virus from Trinidadian ticks and terns. J. Med. Entomol. 5:501-503.
2. CAMIN, J. H. 1963. Relations between host-finding behavior and life histories in ectoparasitic Acarina. Adv. Acarology 1:411-424.
3. CASALS, J. 1970. Antigenic properties of tick-borne viruses: present state of knowledge. Misc. Publ. Entomol. Soc. Amer. 6:327-329.
4. CASALS, J., B. E. HENDERSON, H. HOOGSTRAAL, K. M. JOHNSON, and A. SHELOKOV. 1970. A review of Soviet viral hemorrhagic fevers, 1969. J. Infect. Dis. 122:437-453.
5. CLARK, G. E., C. M. CLIFFORD, L. FADNESS, and E. K. JONES. 1970. Contributions to the ecology of Colorado Tick Fever virus. J. Med. Entomol. 7:189-197.
6. CLIFFORD, C. M., L. A. THOMAS, L. E. HUGHES, G. M. KOHLS, and C. B. PHILIP. 1968. Identification and comparison of two viruses from isolated ticks of the genus Ornithodoros. Am. J. Trop. Med. Hyg. 17:881-885.
7. GARCIA, R. 1965. Collection of Dermacentor andersoni (Stiles) with carbon dioxide and its application in studies of Colorado Tick Fever virus. J. Trop. Med. Hyg. 14:1090-1093.
8. HOOGSTRAAL, H. 1966. Ticks in relation to human disease caused by viruses. Annu. Rev. Entomol. 11:261-308.

9. HOOGSTRAAL, H. 1967. Tickborne hemorrhagic fevers, encephalitis and typhus in USSR and southern Asia. Exp. Parasitol. 21:98-111.
10. HOOGSTRAAL, H., M. N. KAISER, M. A. TRAYLOR, S. GABER, and E. GUINDY. 1961. Ticks (Ixodoidea) on birds migrating from Africa to Europe and Asia. Bull. W. H. O. 24:197-212.
11. HOOGSTRAAL, H., M. N. KAISER, M. A. TRAYLOR, E. GUINDY, and S. GABER. 1963. Ticks (Ixodoidea) on birds migrating from Europe and Asia to Africa, 1959-1961. Bull. W. H. O. 28:235-262.
12. HOOGSTRAAL, H., M. A. TRAYLOR, S. GABER, G. MALAKATIS, E. GUINDY, and I. HELMY. 1964. Ticks (Ixodoidea) on migrating birds in Egypt, spring and fall, 1962. Bull. W. H. O. 30:355-367. 1964.
13. HORSFALL, F. L., JR., and I. TAMM, eds. 1965. Viral and rickettsial infections of man, 4th ed. J. B. Lippincott Co., Phila. xvi + 1282 p.
14. KAISER, M. N. 1966. Viruses in ticks. I. Natural infections of Argas (Persicargas) arboreus by Quaranfil and Nyamanini viruses and absence of infections in A.(P.) persicus in Egypt. Am. J. Trop. Med. Hyg. 15:964-975.
15. KAISER, M. N. 1966. Viruses in ticks. II. Experimental transmission of Quaranfil virus by Argas (Persicargas) arboreus and A.(P.) persicus. Am. J. Trop. Med. Hyg. 15:976-985.
16. KOKERNOT, R. H., C. H. CALISHER, L. J. STANNARD, and J. HAYES. 1969. Arbovirus studies in the Ohio Mississippi Basin, 1964-1967. VII. Lone star virus, a hitherto unknown agent isolated from the tick Amblyomma americanum (Linn.). Am. J. Trop. Med. Hyg. 18:789-795.
17. L'VOV, D. K., A. A. TIMOFEEVA, L. GROMASHEVSKY, and V. I. CHERNOVSKY. 1970. Isolation of arboviruses from Ixodes (Ceratixodes) putus Pick Camb. ticks collected in a bird colony on Tyuleniy Island, Okhotsk Sea. Vopr. Virusol. 15:440-444.
18. LOEW, J., A. RADDA, G. PRETZMANN, and G. STUDYNKA. 1964. Untersuchungen in einem naturherd der Fruhsommer-Meningo-Encephalitis (FSME) in Niederosterreich. 4. Mitteilung: Ergebnisse der okologische untersuchungen an einer population von Ixodes ricinus in jahre 1963. Zentralbl. Bakteriol. Parasitenkd., Infektionskr. Hyg. Abt. I., Orig. 194:133-146.
19. MACLEOD, J. 1962. Ticks and disease in domestic stock in Great Britain. Pages 29-50 *in* Aspects of disease transmission by ticks. Sympos. No. 6., Zool. Soc. Lond.
20. MILNE, A. 1943. The comparison of sheep tick populations. Ann. Appl. Biol. 30:240-250.
21. MILNE, A. 1945. The ecology of the sheep tick, Ixodes ricinus L.; the seasonal activity in Britain with particular reference to northern England. Parasitology 36:142-152.
22. MILNE, A. 1945. The ecology of the sheep tick, Ixodes ricinus L.; host availability and seasonal activity. Parasitology 36:153-157.
23. MILNE, A. 1946. The ecology of the sheep tick, Ixodes ricinus L.; distribution of the tick on hill pasture. Parasitology 37:75-81.
24. MILNE, A. 1948. The ecology of the sheep tick, Ixodes ricinus L.; host relationships of the tick. Part 2. Observations on hill and moorland grazings in northern England. Parasitology 39:173-197.
25. MILNE, A. 1950. The ecology of the sheep tick, Ixodes ricinus L.; microhabitat economy of the adult tick. Parasitology 40:14-34.
26. NUORTEVA, P., and H. HOOGSTRAAL. 1963. The incidence of ticks on migratory birds arriving in Finland during the spring of 1962. Ann. Med. Exp. Biol. Fenn. 41:457-468.
27. OKER-BLOM, N., A. SALMINEMA, M. BRUMMER-KORVENKONTIO, L. KAARIANEN, and P. WECKSTROM. 1964. Isolation of some tick-borne viruses from Ixodes ricinus ticks in Finland Ann. Med. Exp. Biol. Fenn. 42:109-112.
28. POSPELOVA-SHTROM, M. V. 1953. Ornithodorini ticks and their epidemiological significance. Moscow. 235 p. (In Russian).
29. PRETZMANN, G., J. LOEW, and A. RADDA. 1963. Untersuchungen in einem Naturherd der Fruhsommer-Meningo-Encephalitis (FSME) in Niederosterreich. 3. Mitteilung: Versuch einer besamtderstellung des Zyklus der FSME in Naturherd. Zentralbl. Bakteriol. Parasitenkd. Infektionskr. Hyg. Abt. I., Orig. 190:299-312.
30. PRETZMANN, G., A. RADDA, and J. LOEW. 1964. Studien zur Okologie von Ixodes ricinus L. in einem Endemiegebiet der Fruhsommer-Meningo-Encephalitis (FSME) im Bezirk Neunkirchen Niederosterreich). Z. Morphol. Okol. Tiere 54:397-413.
31. PRETZMANN, G., A. RADDA, and J. LOEW. 1964. Untersuchungen in einem Naturherd der Fruhsommer-Meningo-Encephalitis (Tickborne Encephalitis) in Niederosterreich. 5. Mitteilung: Weitere Untersuchungen des Virus Kreislaufes im Naturherd. Zentralbl. Bakteriol. Parasitenkd. Infektionskr. Hyg., Abt. I., Orig. 194:431-439.
32. RADOVSKY, F. J., D. STILLER, H. N. JOHNSON, and C. M. CLIFFORD. 1967. Descriptive notes on Ornithodoros ticks from gull nests on the Farallon Islands and isolation of a variant of Hughes virus. J. Parasitol. 53:890-892.
33. SMITH, C. E. G. 1962. Ticks and viruses. Pages 199-221 *in* Aspects of disease transmission by ticks. Sympos. No. 6. Zool. Soc. Lond.
34. SMITH, C. E. G., M. G. R. VARMA, and D. MC MAHON. 1964. Isolation of louping ill virus from small mammals in Aryshire, Scotland. Nature 203:992-993.
35. SMITH, C. N., M. N. COLE, and H. K. GOUCK. 1946. Biology and control of the American dog tick. U.S. Dep. Agric. Tech. Bull. 905. 74 p.
36. SONENSHINE, D. E. 1970. Current studies on tick biology in relation to disease in the Americas. Misc. Publ. Entomol. Soc. Am. 6:352-358.
37. SONENSHINE, D. E., E. L. ATWOOD, and J. L. LAMB, JR. 1966. The ecology of ticks transmitting Rocky Mountain spotted fever in a study area in Virginia. Ann. Entomol. Soc. Am. 59:1234-1262.
38. SONENSHINE, D. E., and G. M. CLARK. 1968. Field trials on radioisotope tagging of ticks. J. Med. Entomol. 5:229-235.
39. WAHAB, K. S. E. A., R. E. WILLIAMS, and M. N. KAISER. 1970. Viruses in ticks IV. Viruses isolated in Egypt during 1968. Folia Parasitol. (Prague) 17:355-358.
40. WALTON, G. A. 1969. Observations on Ixodes ricinus and louping ill virus in Ireland. Pages 601-608 *in* Proc. 2nd Int. Congr. Acarology.
41. WALTON, G. A., and R. C. KENNEDY. 1966. Tickborne encephalitis virus in southern Ireland. Brit. Vet. J. 122:427-434.
42. WILLIAMS, R. E., K. S. E. ABDEL WAHAB, and H. HOOGSTRAAL. 1970. Viruses in ticks. V. Viruses isolated from Afghanistan ticks during 1968. Folia Parasitol. (Prague) 17:359-366.
43. YUNKER, C. E. 1970. Worldwide research on human and animal diseases caused by tickborne viruses. Misc. Publ. Entomol. Soc. Am. 6:330-338.