Electrophoretically detectable protein variation in natural populations of the lone star tick, *Amblyomma americanum* (Acari: Ixodidae)

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Nine populations of *Amblyomma americanum* (L.) were examined electrophoretically for variation of 21 enzymes. Only three enzymes were not polymorphic and the average heterozygosity per individual (h) for the species was 0.085 with a range of 0.077 to 0.110, comparing well with values in other arthropods. The average Nei identity value for pairwise comparisons among the nine populations was high, 0.994 ± 0.004 ($I \pm SD$). These high identity values and the absence of geographic structuring of the protein variation suggest that this species is genetically homogeneous. Normal levels of genic variability within and a lack of divergence between populations were not predicted by models developed to describe these genetic characteristics on the basis of the heterogeneities encountered by parasites in their environment. An analysis of data from several different species of ticks suggests host mobility and abundance, as well as tick abundance and selectivity in choosing a host, are important parameters in determining genetic variation in these ectoparasites.

INTRODUCTION

The questions of how much genetic variability occurs in species of ectoparasites and how that variation is distributed among populations have received little attention. Mayr (1963) and White (1978) pointed out the trend that evolutionary divergence has proceeded more extensively in parasite groups that were selective in their host preference than in groups that exhibited a non-particular host selection. Price (1977; 1980) defined a parasite by the immediacy of the relationship between individual organisms and a single host (rather than the degree of feeding preference of the parasite species) and applied the theory of fitness sets and adaptive functions (Levins, 1962; 1963; 1968) and environmental grain (MacArthur and Levins, 1964) to conclude that genetic variation within populations of parasites would be small and variability between populations of parasites would be large.

Empirical evidence that addresses the issue of genetic variability in ticks has tended to support Price's ecological view. Wallis and Miller (1983) examined three populations of two species of *Ornithodoros* ticks electrophoretically for nine enzymes. They found within-population heterozygosity values generally less than 5 per cent. Bull

et al. (1984) analysed enzymes electrophoretically in 65 populations representing six Australian reptile tick species of the genera *Aponoma* and *Amblyomma*. The heterozygosity values they reported for these six species were all less than 2.5 per cent. The heterozygosities reported by these authors are very low when compared to a value of 11.2 per cent presented by Nevo (1978) as the average for invertebrates.

The degree of inter-population divergence within species observed in these studies was smaller than predicted by Price's (1977) theory. The genetic identity (Nei, 1972) between conspecific populations of *Ornithodoros* ticks (not reported, but calculated by us from data reported by Wallis and Miller (1983)) was 0.983. Bull *et al.* (1984) reported genetic identities between conspecific populations of reptile ticks that were greater than 0.940. For comparison, the maximum value for the Nei identity statistic (I) is 1.0 and Ayala *et al.* (1975) list an average genetic identity of 0.970 for comparisons of conspecific populations, a value of 0.795 for between subspecies comparisons, and 0.352 for interspecific comparisons.

In contrast to the results of these studies, the average heterozygosity observed in five temporal and geographic populations of *Ixodes ricinus* (L.)

for α -glycerophosphate dehydrogenase was 53.3 per cent $\pm$ 1 per cent (Healy, 1979b) and the average heterozygosity calculated by us as the arithmetic mean of values published for phosphoglucose mutase was 66.9 per cent $\pm$ 2.4 per cent (Healy, 1979a). Although Healy was reporting genetic studies and must have worked with the most polymorphic loci he found, neither theory nor empirical results predicted these high heterozygosity values. Nor does the theory explain observations on *Boophilus microplus* (Canestrini) (Sattler *et al.*, in press). For the 23 enzymes studied in natural populations or recently established colonies from eight North American localities, the average heterozygosity was 9.1 per cent $\pm$ 0.8 per cent, twice those previously reported in population comparisons in other ticks. The average genetic identity between the eight *B. microplus* populations did not conform to theoretical predictions either, although the high values ($I = 0.985 \pm 0.013$) did agree well with results of the other tick comparisons.

The purpose of the present study was to determine how much genetic variation occurs in the lone star tick, *Amblyomma americanum* (L.), and how it is distributed across the species range. The results of the electrophoretic examination are compared to those reported for the other species and differences discussed in the light of Price's (1977) theory. This comparison is appropriate because *Amb. americanum* is in the same sub-family as the Australian reptile ticks and all are three-host ticks (*i.e.*, each of their three life stages, larva, nymph, and adult, feeds on a different host). The lone star tick differs from the reptile ticks in being one of the few truly non-particular feeders among the ticks (Hoogstraal and Aeschlimann, 1982). *Boophilus* is not as closely related, but is a Metastriate hard tick that, like the reptile ticks, has a high degree of host specificity and infests large mammals as does *Amb. americanum*. Since *Ornithodoros* species are soft ticks whose biology differs substantially from that of the Metastriate ticks, they will not be discussed in detail.

MATERIALS AND METHODS

During the summer of 1984, samples of *Amb. americanum* (adults and nymphs) were obtained, either by the authors or from cooperators, at nine localities throughout the species range (fig. 1). The nine localities, identity code, and numbers of each sex obtained from each are as follows: Texas Tech University Center at Junction, Texas (JT; 50 ♀, 25 ♂); Henke Ranch, N. of Kerrville, Texas (KT,

141 ♀, 10 ♂); Bastrop State Park, Bastrop, Texas (BT; 16 ♀, 1 ♂); Cameron, Oklahoma (OK; 84 ♀, 51 ♂); Land Between the Lakes®, Kentucky (KY; 56 ♀, 41 ♂); Camp Blanding, Florida (FL; 24 ♀, 11 ♂); McClellanville (1 ♀, 2 ♂) and Greeleyville, South Carolina (SC; 23 ♀, 13 ♂); Blackstone, Virginia (VA; 41 ♀, 24 ♂); Colts Neck, New Jersey (NJ; 46 ♀, 40 ♂). As samples were obtained, the adults were placed into mating chambers made by gluing stockinette sleeves onto the sides of Hereford steers held in stanchions. When the ticks had fed, they were stored in liquid nitrogen until used for electrophoretic analysis. Nymphs were fed immediately on a steer, held in incubators at 24°C, 85 per cent RH and 12 hour light: 12 hour dark photoperiods until they molted, and these adults were then treated as described above.

The method of preparation of ticks for electrophoresis and electrophoretic procedures were those standard for this laboratory (Sattler *et al.*, in press). Electrophoretic conditions were modified to maximise band resolution. The enzymes examined and the buffers used to resolve them are as follows: Tris-Citric pH = 8.1 buffer (Buffer C of Hilburn and Rai, 1981): Inorganic Pyrophosphatase (PP, EC 3.6.1.1, 1 zone of staining), Hexokinase (HK, 2.7.1.1, 2 zones), Pyruvate Kinase (PK, 2.7.1.40, 1 zone) and Adenylate Kinase (ADK, 2.7.4.3, 1 zone); Tris-Citric pH = 6.7 buffer (the continuous tris-citrate I of Sealander *et al.*, 1971): Isocitrate Dehydrogenase (IDH, 1.1.4.2, 2 zones) and Malic Enzyme (ME, 1.1.1.40, 1 zone); Tris-Glycine buffer (Buffer D of Hilburn, 1980): Peptidase (PEP, 3.4.11, 1 zone); Lithium Hydroxide buffer (LiOH Buffer of Sealander *et al.*, 1971): Esterase (EST, 3.1.1.1, 2 zones); N-(3-Amino-propyl)-Morpholine-Citric pH = 6.5 buffer (Clayton and Tretiak, 1972): Malate Dehydrogenase (MDH, 1.1.1.37, 2 zones), Catalase (CAT, 1.11.1.6, 1 zone), and Phosphoglucose Isomerase (PGI, 5.3.1.9, 1 zone); N-(3-Amino-propyl)-Morpholine-Citric pH = 7.0 buffer: α -Glycerophosphate Dehydrogenase (α GPD, 1.1.1.8, 1 zone), Aconitase (ACON, 4.2.1.3, 2 zones), Triosephosphate Isomerase (TPI, 5.3.1.1, 1 zone), Lactate Dehydrogenase (LDH, 1.1.1.27, 1 zone) and Glutamate Dehydrogenase (GDH, 1.4.1.3, 1 zone).

The females of each population were electrophoresed first and for all enzyme systems. Males, being smaller than females, gave poor results if diluted sufficiently to study all enzymes. Therefore, males were examined for only those enzymes shown to be polymorphic in females of the same population.

Figure 1 The range of *Amblyomma americanum* (after Bishopp and Trembley, 1945) in the United States. Solid dots are the collection sites from which came the samples analyzed for isozyme variation. Identification codes are defined in text.

RESULTS

The procedure given above yielded electromorph information on 21 presumed gene products in 16 enzyme systems. HK-1 and TPI-1 yielded no variants in any population. LDH, CAT, MDH-1 and -2, IDH-1 and -2, PEP, ME, PGI and α GPD exhibited 3-banded heteromorphous phenotypes typical of dimeric proteins. The other proteins, including ACON-A and -C, ADK, PK, HK-2, GDH, PP and EST-2 and -3 had 2-banded heteromorphous patterns typical of monomeric proteins. In PGI and ADK, only females exhibited a heteromorphous pattern; males were always homomorphous. Since in *Amb. americanum* females are XX and males are XO (Oliver, 1977), the electrophoretic results can be explained if PGI and ADK are sex-linked. This explanation has been confirmed by Mendelian analysis (Sattler and Hilburn, unpublished data). The other enzymes exhibited autosomal inheritance.

For calculation of heterozygosities and polymorphisms, an enzyme was considered to be polymorphic if its most common form had a frequency less than 0.99 or if a variant of the enzyme was observed in several populations. Table 1 gives electromorph frequencies for the 19 polymorphic enzymes. HK-1, TPI-1, and LDH were not polymorphic by these criteria. The mean proportion of enzymes polymorphic per population was $P = 0.429$ (range 0.318–0.591). The average observed heterozygosity per locus was $h = 8.5$ per cent (range 7.7 per cent–11.0 per cent).

The variation among these enzymes was not evenly distributed across the range of the species. ACON-A, MDH-2, IDH-2, GDH, PK, and PP were more polymorphic in populations east of the Mississippi River than in populations west of the river. MDH-1 and PEP were more polymorphic in the west. ADK allozyme 0.60 was found only in the west, allozyme 0.91 was found only in the east, and both forms were present in the Kentucky popu-

Table 1 Electromorph frequencies of 19 genes polymorphic in natural *Amblyomma americanum* populations. Population identification codes refer to text.

	KT	BT	JT	OK	KY	FL	SC	VA	NJ
1. Catalase (CAT)									
1.00	0.972	1.00	0.991	1.00	0.988	0.980	1.00	1.00	0.989
0.58	0.028	—	0.009	—	0.012	0.020	—	—	0.011
<i>N</i>	151	17	57	66	80	25	24	44	45
2. Phosphoglucose Isomerase (PGI)									
1.11	—	—	—	0.005	0.007	—	—	—	—
1.00	0.938	0.952	0.904	0.967	0.938	1.00	0.968	0.972	1.00
0.82	0.062	0.048	0.096	0.028	0.055	—	0.032	0.028	—
<i>N</i>	151	21	75	126	92	35	39	65	86
3. Malate Dehydrogenase, Zone 1 (MDH1)									
1.75	0.003	—	0.008	0.016	0.005	—	—	0.008	—
1.00	0.993	1.00	0.984	0.984	0.984	1.00	1.00	0.992	1.00
0.25	0.004	—	0.008	—	0.011	—	—	—	—
<i>N</i>	151	21	62	126	97	31	39	61	82
4. Malate Dehydrogenase, Zone 2 (MDH2)									
1.12	0.003	—	—	—	—	—	—	—	—
1.08	—	—	—	—	—	0.014	—	—	—
1.00	0.990	1.00	0.984	0.988	0.979	0.971	0.949	0.967	0.970
0.85	—	—	—	—	—	0.014	—	—	—
0.69	0.007	—	0.016	0.012	0.021	—	0.051	0.033	0.030
<i>N</i>	147	21	63	126	97	35	39	61	84
5. Peptidase (PEP)									
1.15	0.050	0.042	0.026	0.021	0.039	0.015	—	0.019	—
1.00	0.896	0.916	0.947	0.911	0.894	0.971	0.979	0.971	0.967
0.85	0.054	0.042	0.026	0.068	0.050	0.015	0.021	0.010	0.022
0.70	—	—	—	—	0.017	—	—	—	0.011
<i>N</i>	140	12	57	96	90	34	24	52	46
6. Aconitase, Cathodal Zone (ACON-C)									
1.61	0.003	—	—	—	0.005	—	0.013	0.008	—
1.33	0.430	0.333	0.473	0.390	0.313	0.294	0.346	0.258	0.265
1.16	—	—	—	—	—	—	—	—	0.006
1.00	0.550	0.667	0.500	0.610	0.682	0.706	0.577	0.718	0.729
0.22	0.017	—	0.027	—	—	—	0.064	0.016	—
<i>N</i>	150	21	75	105	96	34	39	62	85
7. Aconitase, Anodal Zone (ACON-A)									
1.05	—	—	—	—	—	0.014	—	0.010	0.033
1.00	1.00	1.00	1.00	1.00	1.00	0.986	1.00	0.990	0.967
<i>N</i>	143	21	69	127	92	35	38	50	76
8. Malic Enzyme (ME)									
1.57	0.003	0.094	—	0.004	0.011	—	0.042	0.010	0.072
1.00	0.997	0.906	1.00	0.996	0.989	1.00	0.958	0.990	0.928
<i>N</i>	151	16	67	125	94	33	24	51	84
9. Isocitrate Dehydrogenase, Zone 1 (IDH1)									
1.33	—	—	—	0.028	0.005	—	—	—	—
1.00	1.00	1.00	1.00	0.972	0.995	1.00	1.00	1.00	1.00
<i>N</i>	143	13	51	125	94	32	24	37	66
10. Isocitrate Dehydrogenase, Zone 2 (IDH2)									
1.28	0.003	—	—	—	—	0.015	—	—	0.012
1.00	0.994	1.00	1.00	0.986	0.979	0.955	0.938	0.979	0.953
0.88	0.003	—	—	0.014	0.021	0.030	0.062	0.011	0.035
0.76	—	—	—	—	—	—	—	0.011	—
<i>N</i>	151	16	61	104	94	33	24	47	85

Table 1—continued

	KT	BT	JT	OK	KY	FL	SC	VA	NJ
11. α -Glycerophosphate Dehydrogenase (α GPD)									
1-75	—	—	—	0-004	—	—	—	—	—
1-55	0-014	—	—	0-036	0-007	0-015	—	—	—
1-00	0-986	0-974	1-00	0-956	0-993	0-956	1-00	0-992	1-00
0-80	—	0-026	—	0-004	—	0-029	—	0-008	—
N	73	19	58	126	73	34	24	61	81
12. Hexokinase, Zone 2 (HK2)									
1-07	0-010	—	—	0-008	0-011	0-059	—	—	0-047
1-00	0-957	1-00	1-00	0-877	0-962	0-941	1-00	0-992	0-942
0-93	0-030	—	—	0-111	0-022	—	—	0-008	0-012
0-78	0-003	—	—	0-004	0-005	—	—	—	—
N	150	19	68	126	91	34	28	65	86
13. Adenylate Kinase (ADK)									
1-00	0-996	1-00	0-992	1-00	0-970	1-00	1-00	0-991	1-00
0-91	—	—	—	—	0-023	—	—	0-009	—
0-60	0-004	—	0-008	—	0-001	—	—	—	—
N	135	21	75	126	85	35	39	65	86
14. Pyruvate Kinase (PK)									
1-06	—	—	0-007	—	—	0-059	—	0-008	0-029
1-00	1-00	1-00	0-993	1-00	1-00	0-941	1-00	0-992	0-971
N	150	21	75	126	96	34	35	65	86
15. Glutamate Dehydrogenase (GDH)									
1-10	—	—	—	—	—	0-039	—	—	0-038
1-00	1-00	1-00	1-00	1-00	1-00	0-961	1-00	1-00	0-962
N	146	18	75	107	38	26	32	39	65
16. Inorganic Pyrophosphatase (PP)									
1-07	—	—	—	—	—	—	—	—	0-238
1-00	1-00	1-00	1-00	1-00	1-00	1-00	1-00	1-00	0-762
N	141	16	61	107	52	33	18	50	61
17. Esterase, Zone 1 (EST 1)									
1-07	0-119	0-143	0-219	0-046	0-092	0-125	0-212	0-266	0-113
1-00	0-416	0-286	0-488	0-389	0-357	0-354	0-365	0-328	0-425
0-91	0-327	0-429	0-195	0-361	0-429	0-333	0-096	0-250	0-330
0-85	0-138	0-143	0-098	0-204	0-122	0-188	0-327	0-156	0-132
N	113	14	41	54	49	24	26	32	52
18. Esterase, Zone 2 (EST 2)									
1-03	0-046	0-048	0-041	0-102	0-033	0-015	0-108	0-109	0-049
1-00	0-383	0-452	0-628	0-426	0-225	0-500	0-378	0-464	0-377
0-97	0-520	0-452	0-308	0-361	0-642	0-485	0-392	0-345	0-500
0-87	0-051	0-048	0-027	0-111	0-100	—	0-122	0-082	0-074
N	106	21	74	108	60	33	37	55	81

lation. Finally, for IDH-1, an infrequent allozyme was found in Oklahoma and Kentucky, but was not observed in any other sample. Because none of the uncommon variants of these enzymes had high frequencies, the data were significantly heterogeneous ($P < 0.001$) as determined by a test for homogeneity among frequencies (Snedecor and Cochran, 1967), but there was no significant difference between pooled electromorph frequencies from the western and eastern populations, using a t-test for the difference between two frequencies (Sokal and Rohlf, 1969). Thus, separate populations differ from the species as a whole,

but no geographically defined group of samples differed from the others.

The enzymes CAT, ACON-C, EST-2, and EST-3, the latter three being the most polymorphic in the study, revealed no geographic patterns in the frequencies of their electromorphs. The differences among these enzymes seemed to result more from random effects and the vagaries of sampling the gene pools.

An analysis of enzyme similarities among populations of *Amb. americanum* was performed using a personal computer computation (Sattler and Hilburn, 1984) of Nei's (1972) identity statistic

Figure 2 The dendrogram reflecting isozyme similarities among nine populations of *Amblyomma americanum* produced by submitting Nei identity values to an unweighted pair-group clustering procedure using arithmetic averages (U.P.G.M.A.). For population identity codes refer to text.

with modifications by Nei (1978), Mueller and Ayala (1982), and Hillis (1984). The results are summarised in a dendrogram (fig. 2) obtained by submitting the pair-wise identities to an unweighted pair-group method of clustering using arithmetic averages (UPGMA, Sneath and Sokal, 1973).

Two results are striking. First, the mean identity for all possible comparisons was very high at 0.9942 ± 0.0044 ($I \pm SD$). The smallest average identity value between any clusters in the phenogram was only 0.990. In fact, the smallest identity value between any two populations was 0.979, that between Junction, TX, and Kentucky.

A second result is that there was no clear geographic pattern in the genetic variation. Whatever the meaning of the patterns observed in electromorph frequencies of MDH-2, IDH-2, and PEP, and the minor polymorphic genes, the differences were not great enough to affect the clustering of the populations. There is clearly no relationship between geographic distance and genetic identity values.

Another method for estimating the amount of interpopulation divergence relative to intrapopulation variation is by comparing the F-statistics (Wright, 1951) evaluated from enzyme data. Using the nine geographic samples as subdivisions of *Amb. americanum*, the F-statistics were calculated for all 21 enzymes by the procedure of Weir and Cockerham (1984). The value for F_{IT} (correlation

between two gametes united to produce an individual relative to the total population) was 0.089 ± 0.036 ($X \pm SD$); the value for F_{IS} (correlation between two gametes united to produce an individual relative to its subdivision) was 0.054 ± 0.051 , and the value of F_{ST} (the correlation between two gametes drawn randomly from different subpopulations) was 0.037 ± 0.020 . The statistic F_{ST} measures the genetic differentiation between populations. The low value of F_{ST} compared to F_{IT} and F_{IS} further suggests a lack of interpopulation divergence over the range of *Amb. americanum*.

DISCUSSION

The empirical evidence obtained from electrophoretic studies of *Amb. americanum* populations does not match the patterns Price's (1977) model predicts for a parasitic species: "small, relatively homozygous populations with little gene flow between populations, which results in many specialised races, rapid evolution, and speciation without geographic isolation, and an abundance of sibling species" (Price, 1977). Instead the lone star tick is revealed as a variant rich species that exhibits little interpopulation divergence. Certain populations, e.g., that from New Jersey, have both qualitative and quantitative allozyme characteristics that distinguish them, but in no case do these differences seem sufficiently unique as to suggest true genetic divergence. Instead, these differences appear to result from local, probably transitory, chance events; perhaps even resulting from the vagaries of sampling a genetically undifferentiated species.

Earlier electrophoretic studies had suggested that ticks carried little intraspecific isozyme variation (Wallis and Miller, 1983; Bull *et al.*, 1984; Hunt and Hilburn, 1985). With a broader sampling of a species, the use of a greater number of electrophoretic conditions, and the examination of larger sample sizes, the present study has found only two enzymes (HK-1 and TPI-1) for which there was not at least one variant and only one other enzyme (LDH) that could not be classified as polymorphic by the criteria commonly used. The mean proportion of enzymes polymorphic per population, $P = 0.429$ in *Amb. americanum*, compares well with those observed in other arthropods (Nevo, 1978) and is slightly higher than the value $P = 0.33$ observed in *Boophilus microplus* (Sattler *et al.*, in press). However, it is much higher than values obtained for Australian reptile ticks (range:

0 to 0.085; Bull *et al.*, 1984) or in *Ornithodoros* (range: 0.111–0.222; Wallis and Miller, 1983). The average observed heterozygosity per locus, $h = 0.085$, is similarly comparable to values of h in other arthropods and the value $h = 0.092$ observed in *B. microplus*, but is much higher than values from other ticks. The comparatively high levels of intrapopulation variation observed in *Amb. americanum* are not predicted by Price's (1977) model of the distribution of genetic variation in parasites, and in this regard these data also differ from those reported in other tick species.

The high values of genetic identity and low value of F_{ST} compared to F_{IS} and F_{IT} that were obtained from these enzyme comparisons suggest that genetic variability in this species is generally evenly distributed over the species range, a result that appears general in the ticks so far examined. Both qualitative and quantitative differences do occur. The New Jersey population had a unique form of PP and the Florida population had two forms of MDH-2 not found in other samples. There were forms of ACON-A and GDH present in population from the southeastern United States, but absent from those populations from Texas and Oklahoma. The genes MDH-2, IDH-2, and PK were more polymorphic in the former populations while PEP and MDH-1 were more polymorphic in the latter. These differences argue for a small degree of geographic structuring, but they were not large enough to affect the measures of genetic relatedness. In fact, studying the gene-by-gene identity comparisons of pairs of populations has revealed that the observed clustering is more the result of lack of geographic structure in the variability of the very heteromorphic ACON-C, EST-2, and EST-3. These enzymes were responsible for lowered interpopulation identity values and their effects generally swamped those attributable to other enzymes. Since there were no recognisable trends in the geographic distributions of allozymes of these latter three enzymes, there were no patterns in the separation of populations. Thus, the high degree of raceation predicted by Price's (1977) model is not observed in *Amb. americanum* nor any other tick so far examined.

In part, the inability of Price's (1977) model to predict the distribution of genic heterozygosity in *Amb. americanum* may be because this tick does not meet the definition of a parasite upon which Price's arguments are based. There is no permanent association between an individual tick and a single host. Each lone star tick attaches to and feeds on three hosts during its lifetime but leaves each to molt or lay eggs on the ground. Not only can

individual *Amb. americanum* not coevolve with a single host, but because the three life stages of the tick are seldom spent on the same order of vertebrate much less of the same species, this tick species cannot coevolve with a single host species. This life history would argue against the subdivision of the species that would lead to the homozygosity, specialisation, and raceation predicted by Price's (1977) model. Moreover, the passage from host to host in this three-host tick should reduce the probability that siblings would remain together to intermate as adults, so long as hosts are plentiful, thus removing inbreeding as a force promoting homozygosity.

The degree to which populations diverge genetically is primarily determined by the amount of gene flow between them. Even infrequent exchange of genes between populations will prevent genetic divergence as long as the exchange is not solely between close, neighboring populations having very similar gene frequencies (Crow and Kimura, 1970). Since ticks are relatively inactive when they are off the host, the vagility of these parasites, and therefore, the rate of gene flow, depends on host mobility. The absence of genetic divergence between geographical disjunct *Amb. americanum* populations can be explained by its lack of host specificity (ref. Mayr, 1963) and by the mobility of its large hosts, including cattle, deer, and certain rodents and carnivores (Bishopp and Trembley, 1945), all of which can disperse ticks rather broadly. Moreover, the long distance transport of livestock and pets within the range of this tick and the large population sizes encountered throughout its distribution act to reduce interpopulation differentiation.

In summary, *Amb. americanum* is a variant rich species which shows little interpopulation divergence. That these observations do not agree with expectations can be attributed, in part, to the inappropriate application of the model of Price (1977) to generate predictions about ticks. Comparisons of data from *Amb. americanum* to observations on other ticks suggest that the levels of genetic variation within and between populations of hard ticks are best explained in terms of host mobility, population sizes of both hosts and parasites, and the degree of host specificity exhibited by the tick. Phenotypic homeostasis may also be important, but its effects are more difficult to deduce from available data.

Acknowledgements We would like gratefully to acknowledge the assistance of all those colleagues who supplied us with ticks: Dr D. R. Barnard, Lone Star Tick Research Laboratory,

U.S.D.A., A.R.S., Poteau, OK.; Dr R. H. Zimmerman, Land Between The Lakes, Tennessee Valley Authority, Golden Pond, KY.; Dr R. H. Roberts, Insects Affecting Man and Animals Research Laboratory, U.S.D.A., Gainesville, FL.; Dr T. R. Adkins, Jr, Department of Entomology, Fisheries and Wildlife, Clemson University, Clemson, S.C.; Dr T. L. Schulze and M. F. Lakat, New Jersey State Department of Health, Trenton, N.J.; and Drs E. C. Turner and P. J. Semtner, Southern Piedmont Research and Continuing Education Center, Virginia Polytechnic Institute and State University, Blacksburg, VA. We would also like to thank the Texas Parks and Wildlife Department for assistance in collecting on the state parks in Texas, and Dr James Wangberg for facilitating our collecting at the Texas Tech University Center at Junction, TX. Claudio Castillo gave indispensable technical assistance.

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