



Ectoparasitic Mites on Rodents: Application of the Island Biogeography Theory?

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need to build highways. I have calculated this reduced highway need as 4.45 lane-miles (7), and crediting this saving to BART, the freeway-to-rail efficiency ratio changes from 25.2 to 25.1.

Construction-energy is not the entire story, however. One must also consider operating-energy. The operating-energies of BART, buses, and cars are 4740, 2900, and 8310 Btu/PM, respectively, including both propulsion energy and a pro rata share of the energy involved in constructing the vehicle (7). Thus, every-time BART attracts someone away from a car it saves energy but, unfortunately, all rail transit systems steal most of their passengers from the existing bus systems, and this wastes energy. BART has the best auto-diversion (46.5 percent, under very generous assumptions) of any rail system, but even so its net operating-energy saving is only 680 Btu/PM. This operating-energy saving is so small, relative to BART's construction-energy, that it will take 535 years even to repay the energy invested in building the system, much less save any energy. Furthermore, this result is so compelling that even in a transit Nirvana—with double the existing patronage, 75 percent of the passengers coming from cars, and a 50 percent load factor—it would still take 168 years to repay its construction energy.

Rail transit is an energy waster. If we want to improve the efficiency of our transportation systems, we should emphasize the development of more efficient automobiles, because that is where almost all of the existing transportation energy is now being used, and the development of bus-oriented transit systems, because of their energy efficiency.

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It is encouraging to see greater analytical attention being paid to energy flows in the economic system. But the difficulty of analysis and scarcity of good data are not excuses for unwarranted conclusions. Controversial ideas must meet the highest possible standards.

First, Lave asserts that "freeway construction produces 25.2 times more passenger-miles per British thermal unit than rail transit construction." Besides an inappropriate thesis, the statement does not follow from his data. The data refer to California freeways and to BART, a single California electric rail transit system. California is an extremely car-oriented state, and the only realistic way to build successful mass transit systems there would be to occlude car lanes with mass transit lanes. Then we would approach the saturation point in the remaining car lanes and in the mass transit lanes. There is little doubt that, at the saturation flow, mass transit can handle more passenger-miles per hour than automobiles. Our studies show much less capital use per passenger-mile in mass transit systems than in cars. This result alone would indicate that the seat miles per hour (a potential capacity measure) would be greater in mass transit systems than in automobiles. Also, the reaction times for starting and stopping, which control minimum vehicle spacing, apply to vehicles and not passengers. The greater number of vehicles in the auto system means that the minimum total head space of the system at capacity would be greater for cars than for mass transit vehicles. Thus the maximum potential passenger-miles per hour could be achievable with mass transit systems, not highway systems. We pointed out (1) that (i) highway construction was 62 percent more energy-intensive than rail

mass transit construction, per dollar invested (rail construction also required more jobs per dollar); and (ii) that construction costs (excluding land) were slightly greater for a 12-foot-wide highway lane-mile than for a single rail track-mile. Thus, when potential passenger capacity and average U.S. construction techniques are considered, I am forced to conclude the opposite of Lave; that is, more potential passenger-miles per British thermal unit can be delivered by rail systems than by auto systems. But potential right-of-way capacity is not an appropriate basis for comparison. Governmental investment ought to foster the lowest total cost system of those which deliver the same service. The total cost might be based on dollars, energy, or jobs produced, both directly and indirectly, and would include the construction of right-of-way, the construction of vehicles, and the operation and maintenance of the entire system.

Table 2 in (2) showed the costs, per passenger-mile, of various forms of transportation. On an energy basis, electric trains are relatively the most wasteful form because of their poor load factor. But diesel-electric intercity rail transit and diesel bus transit are less energy-intensive than both electric rail and cars. And electric rail transit is less energy-intensive than urban cars, at comparable load factors. Therefore, I again conclude the opposite of Lave—rail transit is not an energy waster. And even if we were not sure of this point, energy policy should direct government transportation investment away from highways and toward rail transit. Existing highways will more than handle the bus traffic.

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In their analysis of a summary (1) of ectoparasitic mite species records for North American cricetid rodents, Dritschilo *et al.* (2) state that the number of mite species on a host is positively correlated with host geographic range, and they interpret their "species area curve" in light of applications (3) of the theory of

island biogeography (4). Dritschilo *et al.* (2) did not properly account for the positive correlation between host geographic range and the intensity with which the host has been studied. Reanalysis of their data shows that their data base is inadequate to demonstrate such a relationship.

For 40 species of cricetid rodents from which mites are listed in (1) [actually (1) lists 43 such cricetid species] (5), Dritschilo *et al.* show a positive correlation ($r = .61$; $P < .001$) between the \log_{10} of the number of species and the \log_{10} of the host geographic range. However, the intensity of research (parasitological and otherwise) on rodent species is positively correlated with geographic range. Widespread species are available for study at many institutions, become important research systems (*Peromyscus maniculatus*, *Microtus pennsylvanicus*), and may assume considerable economic importance (*Ondatra zibethicus*, the muskrat).

To estimate the effects of intensity of research on the number of mite species reported in (1), we counted the number of publications on each host species listed for the four most recent years in a major abstracting service (6). Using $\log(n + 1)$ (7) number of publications for each host species as the independent variable and the \log number of mites as the dependent variable, we found that the correlation coefficient ($r = .69$; $P < .001$; $N = 43$) exceeded that found when geographic range was used as a predictor. Analysis of correlation coefficients of the two untransformed independent variables yields a similar result.

Although our research intensity predictor is more highly correlated with number of mite species than is host geographic range, these correlation coefficients are not significantly different. The 95 percent confidence limits for the former correlation ($r = .61$, $N = 40$) are .33 to .77, and for the latter ($r = .69$, $N = 43$) are .49 to .82 (8).

Partial correlation analysis measures the remaining association between any pair of variables when other variables are held constant (9). If a significant correlation between an independent variable (x_1) and a dependent variable remains significant when a second independent variable (x_2) is held constant, this suggests that x_1 and x_2 have independent significant effects. When host geographic range is controlled for (partialled out) the partial correlation of geographic range and numbers of mites is .43 ($.01 < P < .001$). Partialling out geographic range results in a higher partial correlation, .54 ($P < .001$), for the number of publications and the number of mites. Thus, the amount of research on a species needs to be considered before species lists can be utilized in the construction of species area curves.

This reanalysis of Dritschilo *et al.* suggests that uneven sampling of host "is-

lands" is a serious source of bias. The construction of any species area curve is based on the assumption that the species lists for each "island" represent an accumulation approaching the total number of species on the "island." If this is only true for some "islands," the sampling procedure is inadequate for the development of a species area curve. Proper application of the island biogeography theory usually involves an attempt to census "island" faunas (10).

Other important biases are introduced by Dritschilo *et al.* They omit eight cricetid species for which no mites were reported in (1). Four of these species (11) are widespread, having geographic ranges exceeding 777,000 km². Their "species area curve" omits "islands" with large areas but lacking in reported mite species (2); consequently, both the slope and r are biased in the direction of higher, more statistically significant values. The habits of some cricetid species having wide geographic ranges make collections of these species infrequent in typical small mammal-trapping programs. *Phenacomys longicaudus* is arboreal (12); *Synaptomys* spp. live in bogs and are notoriously trap-shy (13). These species have relatively few reported ectoparasites. Species found almost exclusively at high latitudes (14) and some species (15) with restricted ranges distant from research centers are also likely to be undersampled. Unreported mites from rodents with very small ranges will yield "species area" regression statistics with higher r and lower slopes.

Using the $\log(n + 1)$ transformation for the dependent variable, number of mites per host, and for the independent variable (number of publications), we can include the cricetid species omitted in (2). Again, the number of publications is more highly correlated with number of mite species ($r = .71$; $P < .001$; $N = 51$) than is host geographic range ($r = .60$; $P < .001$; $N = 51$). Partial correlation at $N = 51$ is similar to the analysis for $N = 43$.

The attempt (2) to account for the effect of uneven intensity of research by comparing correlation coefficients of well-studied (*Peromyscus*) and poorly studied (*Microtus*) species area curves fails because searching intensity (as measured by the number of publications) correlates strongly with geographic range among the species used by Dritschilo *et al.* ($r = .70$; $P < .001$; $N = 43$) and among all species ($r = .53$; $P < .001$; $N = 51$). As Dritschilo *et al.* suggest, poorly studied species groups should show a high variance; but the positive relation between intensity of

study and geographic range invalidates their conclusion that lack of study does not introduce artificial correlations into the data.

When suitable data are available the number of parasite species may prove to be correlated with host geographic range. However, the underlying reasons for such correlation are likely to be the greater variety of microhabitats occupied and greater physiological and morphological variability found in many widespread species, rather than "host island equilibrium numbers," geographical overlap of "host islands," and mite species "turnover rates" as suggested (2).

Lynch and Johnson (16) have demonstrated the hazards of published surveys as a source for the estimation of species turnover rates in applications of the island biogeography theory (4). Our present thesis is that the construction of species area curves from species lists may lead to spurious correlations and misapplication of the theory of island biogeography to host-parasite relationships.

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5. Dritschilo *et al.* omit species whose ranges lie mostly south of the U.S.-Mexico border. United
6. *Zoological Record* for 1968-1971. Exceptions in (5) were not included; however, the three species listed in (1) but inexplicably not utilized by (2) were included in our reanalysis.
7. n is the number of publications listed for each species in (6). The $\log(n + 1)$ transformation permits inclusion of zero data points for those rodent species for which no reference was listed in (6).
8. The 95 percent confidence limits were calculated with the use of z transformation, as described in (9).
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10. For example, E. O. Wilson and D. S. Simberloff, *Ecology* **50**, 267 (1969); R. P. Seifert, *ibid.* **56**, 1416 (1975).
11. *Lemmus trimucronatus* (3,504,273 km²), *Microtus miurus* (1,320,901 km²), *Peromyscus nasutus* (1,017,871 km²), *Reithrodontomys montanus* (1,814,815 km²). Our 51 species include all those cricetid species listed in E. R. Hall and K. R. Kelson [*The Mammals of North America* (Ronald, New York, 1959), vol. 2], which were used by Dritschilo *et al.* plus those species for which no mites were reported in (1) but which satisfy the requirement of Dritschilo *et al.* that their ranges lie mostly north of Mexico. Our eight additional species also do not include exclusively insular species (such as *Peromyscus sitkensis*), as none were used by Dritschilo *et al.*, nor do we include *Microtus ludovicianus* which is believed to be extinct.
12. L. G. Ingles, *Mammals of the Pacific States* (Stanford Univ. Press, Stanford, Calif., 1965).
13. W. J. Hamilton, *Mammals of Eastern United States* (Haefner, New York, 1963).

14. *Clethrionomys rutilus*, *Microtus oeconomus*, *Phenacomys intermedius*, *P. silvicola*, *Synaptomys borealis*, *Lemmus trimucronatus*, *Arvicola richardsoni*, *Dicrostonyx torquatus*, *D. hudsonius*.
 15. For example, *Microtus parvulus* (5309 km²) in the eastern Florida panhandle, *Neotoma stephensi* (164,465 km²) in northeastern Arizona and western New Mexico, *Phenacomys silvicola* (6268 km²) along the central Oregon coast.
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We take issue with Kuris and Blaustein's method (1) of analysis. We agree that the number of mite species reported per rodent is a function of intensity of study and noted that some of our sources reflected this fact (2). However, we suggest that the data used by Kuris and Blaustein are not appropriate for analyzing such a bias.

Kuris and Blaustein comment that the number of publications per cricetid species, regardless of the nature of the publications, is correlated with the distributional area of the species. They also state that intensity of searching for ectoparasites can be measured by the number of publications. Such a correlation is not applicable to our data unless it can be demonstrated that the intensity of *mite studies* per cricetid species is correlated with distributional area. Microtines, for example, have been intensively studied with relation to their population dynamics (3) but with little regard for ectoparasites. Of the articles published from 1968 to 1971 and used by Kuris and Blaustein, only 15 dealt in any way with North American acari, a woefully inadequate sample size. Any correlation that may have been constructed from such a small number of publications would certainly have been confounded by the inclusion of numerous studies on aspects of cricetid biology irrelevant to mite faunas.

The intensity of mite studies cannot easily be quantified and related to host areas by merely counting publications even when such publications deal with mite studies. A single publication including species with large and small ranges (4) will often have sample sizes that

would make its study intensity equivalent to numerous other publications. Single publications on mite associates of rodents with small geographic ranges (5) can also include a greater proportion of the host population than all the publications on a species with a larger area combined. However, as most published studies do not indicate numbers of hosts examined, there is no way to determine precisely the intensity of study of rodent mite faunas from the published data. Kuris and Blaustein present no compelling reason whatever to suspect that intensity of study of rodent mites is correlated with host range.

Kuris and Blaustein argue that the omission of eight host species for which no mites were reported constitutes a bias in the direction of more statistically significant results. We feel that the exclusion of these host species is justified as they are the most poorly studied (6). Since very intensive studies (over 10,000 hosts) in northern Scandinavia (7) on similar host groups have yielded numbers of mites per host species predictable on the basis of host range, we feel that a much greater bias would have resulted from the inclusion of the eight unstudied species with no reported mites.

Kuris and Blaustein correctly point out an omission on our part. Two cricetid species were omitted because of differences in nomenclature between our two data sources (8). One species was included in the regression analysis but was inadvertently omitted from Fig. 2a and the discussion in the text. We apologize for these oversights; however, the two omitted species do not appreciably affect our correlation or our conclusions.

The underlying reasons for the correlation between number of mite species and host distributional area are related to two factors, both ultimately relevant to island biogeography theory. Specialist species such as prostigmatid and astigmatid mites track host resources on the basis of similarities in the host-parasite interface (9). Generalists such as most mesostigmatid mites tend to track host resources on the basis of similar host ecol-

ogy (10). Both factors directly affect extinction rates and ultimately rates of species turnover. Wider geographical range of host species provides, in essence, more opportunities for potential colonizing species of both types. Thus, geographical overlap of host islands directly affects the equilibrium number of parasite species.

In conclusion, we agree that care must be taken in the interpretation of species area curves drawn from published surveys and reiterate our claim that "conclusive evidence requires that species turnover rates for host islands be measured" (2). Before such an expensive and time-consuming project can be undertaken, some assurance is required that it might be fruitful. We hope that we have provided sufficient assurance in our report.

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