Iowa Research Online
The University of Iowa's Institutional Repository

Department of Biology Publications

1-1-1981

Species as Islands: Comments on a Paper by Kuris et al.

Stephen D. Hendrix
University of Iowa

John H. Lawton

Howard Cornell

Please see article for additional authors.

Author Posting. Copyright © 1981 The University of Chicago Press. This article is posted here by permission of the publisher for personal use, not for redistribution.

The definitive version was published in *American Naturalist*, 117:4 (1981), pp. 623-627. http://www.jstor.org/stable/pdfplus/2460593.pdf

Hosted by Iowa Research Online. For more information please contact: lib-ir@uiowa.edu.

CHICAGO JOURNALS

The American Society of Naturalists

Species as Islands: Comments on a Paper by Kuris et al.

Author(s): John H. Lawton, Howard Cornell, William Dritschilo, Stephen D. Hendrix

Source: *The American Naturalist*, Vol. 117, No. 4 (Apr., 1981), pp. 623-627
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/2460475
Accessed: 28/09/2010 17:00

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=ucpress.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

The University of Chicago Press and *The American Society of Naturalists* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist.*

http://www.jstor.org

SPECIES AS ISLANDS: COMMENTS ON A PAPER BY KURIS ET AL.

Kuris et al. (1980) review a number of problems associated with treating hosts as islands. While the issues they raise provide a valuable focus for future research, we believe that some of their views are unduly pessimistic. They suggest, for example, that literature surveys are inappropriate for demonstrating species-area phenomena because: (1) Countries are not islands. (2) Areas devoted to the cultivation of crop plants fluctuate annually. (3) Species lists accrue but never delete pest species. (4) Species-area relationships are sampling artifacts because more widespread species receive more investigation. (5) A series of special natural history details muddy the comparison between real islands and the moving, overlapping, growing, potentially toxic islands created by host organisms. (6) Changes in the sizes and ranges occupied by hosts do not result in significant additions to, or deletions from their parasite guilds. Some of these points are dealt with by Rey et al. (1981). Here we focus upon the problem of sampling bias and use of literature surveys; then we look briefly at some of the special host features to which Kuris et al. refer, and finally, examine changes in parasite species-richness as host ranges change in size.

Most existing species-area relationships rely heavily on previously published data. Indeed, without such data the ability of any scientist to test hypotheses and draw broad conclusions would be severely limited. No one person could adequately census all the insects of cacao or sugarcane throughout the world, or all of the mites on several species of rodents. However, by carefully using literature data, the number of tests of interesting hypotheses can be greatly increased.

Kuris et al. refer to data in several studies as "substantially unsuitable," implying instead that species-area relationships are sampling artifacts, generated by underrecording on rare hosts. We think this unduly pessimistic on two grounds. First, in any well-sampled host biota, a correlation between host range and research effort would be a natural consequence of the more protracted sampling required for broadly distributed species. Of course, proportionally greater sampling on broadly distributed species could produce an artificially enhanced correlation, but the tendency for this kind of bias appears rare (O'Connor et al. 1977; Cornell and Washburn 1979). Second, several of the insect-host plant examples which they criticize (Strong 1974; Strong and Levin 1979; Lawton and Schröder 1977) refer to the British Isles, which has the best documented flora and fauna in the world. Victorian naturalists and their modern day counterparts display a fascination for rarities defying rational explanation! Obviously certain insect groups (Lepidoptera for example) are much better documented than others (the pioneer study of Typhlocybine leafhoppers by Claridge and Wilson [1976] is a good example), but there are no grounds for believing that distorted taxonomic coverage is proportionately worse on rare plants. Intense study will always improve and extend host-plant records, but it is extremely unlikely to destroy existing species-area relationships for British plants and their phytophagous insects. One example will suffice. Bracken fern (*Pteridium aquilinum*) was long

Am. Nat. 1981. Vol. 117, pp. 623–627.
© 1981 by the University of Chicago. 0003–0147/81/1704–0025$02.00

assumed to be depauperate in insect species, and its British fauna were comparatively poorly studied. Detailed investigation (Lawton 1976, 1978*a*, 1978*b*; Lawton and Eastop 1975; Rigby and Lawton 1981) shows that 39 species of insects feed on the plant regularly or occasionally in Britain. Despite being poorly studied prior to these investigations, only six of the 39 species (*Bourletiella viridescens, Chirosia albifrons, Philaenus spumarius, Aphis fabae, Macrosiphum ptericolens,* and *Olethreutes lacunana;* see Appendix I in Lawton [1976] for details) are not explicitly recorded in the British entomological and natural history literature prior to 1975 as feeding on bracken, although *C. albifrons* was suspected to. One species, *Mamestra oleracea*, recorded in this early literature, but discounted by Lawton (1976) has since been found abundantly on bracken in southern England. In brief, we believe that published host-plant records are sufficiently reliable to establish broad patterns in species-area relationships for various groups of plants. Of course the amount of variation explained by such relationships varies from case to case (May 1979). Some of this variation is undoubtedly due to the quality of the data (Lawton and Price 1979), and some to the biological phenomena outlined by Kuris et al. However, the fact that additional processes are undoubtedly at work decidedly does not rule out the existence of biologically and statistically significant species-area effects.

For example, Kuris and his coworkers are concerned that the overlapping ranges of different host species may invalidate species-area relationships. In fact, far from confounding such relationships, range overlap is probably one of the key mechanisms by which they are generated (Dritschilo et al. 1975). Range overlap may be important in generating this relationship in the leafminer-Californian oak complex, for example, on an evolutionary rather than ecological time scale (Opler 1974). Phylogenetic propinquity of specialized leafminer species seems more a function of oak species sympatry than oak taxonomic affinity, suggesting higher rates of host shifting in host overlap zones.

Kuris et al. also worry that "other factors influencing parasite species richness may be host species diversity and the degree of phylogenetic similarity of host species" (p. 574). Such factors have been looked for in insect-plant interactions, and contribute rather little to the residual variation around species-area relationships (Cornell and Washburn 1979; Connor et al. 1980; Lawton 1978*a*; Lawton and Price 1979; Southwood 1977; Strong and Levin 1979).

We do not deny that a whole series of processes can, in theory at least, modify and influence species-area relationships. Our point is that data already exist with which to attempt partial, quantitative tests of these effects. We see them as modifying underlying species-area relationships, not destroying them.

Finally, Kuris et al. imply that parasite species-richness is not known to change appreciably as host ranges expand or contract. The apparent lack of extinctions among the parasites of the gray whale (*Eschrichtius robustus*) is an excellent case in point.

Gray whales now occur only in the North Pacific and adjacent waters of the Arctic Ocean. There are presently two geographically isolated stocks; an eastern Pacific stock which migrates between breeding areas off Baja California and

wintering grounds in the Bering and Chukchi Seas, and a western Pacific stock which migrates in a similar way between South Korea and the Okhotsk Sea (Reilly et al. 1980; Zimushko and Ioashin 1980). We agree with Kuris et al. that the western Pacific stock is now extremely small (Anon. 1980). We disagree with their suggestion that the eastern Pacific stock was reduced to "a few hundred individuals by the early 1900's" (p. 579). Calculations by Ohsumi (1976) "suggest that the stock attained its lowest size of 4,400 in 1875" (Reilly et al. 1980, p. 359). Total eastern Pacific stock probably never exceeded 15,000 before harvesting.

According to Kuris et al. the gray whale has four species-specific ectoparasites, none of which have become extinct as the population declined. They believe that species-area theory predicts there should have been some extinctions. We are less sure. Changes in numbers say nothing about changes in geographical range: A species may decline in numbers while continuing to occupy much of its former range at reduced densities. We can therefore leave aside the question of how much Pacific populations of gray whales have actually declined (it appears to be less than Kuris et al. imply; certainly the matter is debatable), and focus instead on contraction of range. The gray whale no longer breeds in all the places it used to; hence its breeding range has contracted. However, it moves each year over huge distances, so that its total geographical range was, and still is, enormous. At best (or worst), if the western Pacific stock were extinct (it is not) the total range of the species may have been roughly halved (R. Gambell, personal communication to J. H. L.). Given a standard species(S)-area(A) relationship of the form $S = cA^z$, with $z = 0.3$ (Connor and McCoy 1979), we would therefore predict an extinction of ectoparasites of at most three-quarters of a species ($4 \times 0.5^{0.3}$, i.e., from 4 to 3.25). In other words, it is not sufficient to observe a decline in host range and automatically predict extinctions in its parasite fauna. Lack of any extinctions may still be compatible with existing theory.

The data for insects on host plants provide numerous well-documented extinctions as host ranges and habitats contract, and colonizations as they expand. The interested reader is referred to Hawksworth (1974), Southwood (1961), Strong (1979), Ward (1977), and Winter (1974).

There is one last point. Species-area relationships are empirical patterns: To find them, or to look for them in no way implies acceptance of the MacArthur-Wilson theory of island biogeography (MacArthur and Wilson 1967). Where species-area relationships are observed they may be generated by one or more of several possible mechanisms (Connor and McCoy 1979). We are optimistic that the mechanisms generating species-area relationships for parasites on hosts will become increasingly well understood over the next decade and supported by experimental tests.

ACKNOWLEDGMENTS

We would like to thank Ray Gambell of the International Whaling Commission and John Beddington for making the data on gray whales available to us prior to publication.

LITERATURE CITED

Anonymous. 1980. Gray whales. Report of the sub-committee on protected species and aboriginal whaling. Rep. Int. Whaling Comm. 30:104–105.

Claridge, M. F., and M. R. Wilson. 1976. Diversity and distribution patterns of some mesophyll-feeding leaf-hoppers of temperate woodland canopy. Ecol. Entomol. 1:231–250.

Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. Am. Nat. 113:791–833.

Connor, E. F., S. H. Faeth, D. Simberloff, and P. A. Opler. 1980. Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. Ecol. Entomol. 5:205–211.

Cornell, H. V., and J. O. Washburn. 1979. Evolution of the richness-area correlation for cynipid gall wasps on oak trees: a comparison of two geographical areas. Evolution 33:257–274.

Dritschilo, W., H. Cornell, D. Nafus, and B. O'Connor. 1975. Insular biogeography: of mice and mites. Science 190:467–469.

Hawksworth, D. L. 1974, editor. The changing flora and fauna of Britain. Systematics Assoc. Special Vol. 6. Academic Press, London.

Kuris, A. M., A. R. Blaustein, and J. J. Alió. 1980. Hosts as islands. Am. Nat. 116:570–586.

Lawton, J. H. 1976. The structure of the arthropod community on bracken. Bot. J. Linn. Soc. 73:187–216.

———. 1978*a*. Host-plant influences on insect diversity: the effects of space and time. Diversity of insect faunas. Symp. R. Entomol. Soc. Lond. 9:105–125.

———. 1978*b*. *Olethreutes lacunana* (Denis & Schiffermüller) (Lepidoptera: Tortricidae) feeding on bracken. Entomol. Gaz. 29:131–134.

Lawton, J. H., and V. F. Eastop. 1975. A bracken feeding *Maerosiphum* (Hem., Aphididae) new to Britain. Entomol. Gaz. 26:135–138.

Lawton, J. H., and P. W. Price. 1979. Species-richness of parasites on hosts: agromyzid flies on the British Umbelliferae. J. Anim. Ecol. 48:619–637.

Lawton, J. H., and D. Schröder. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. Nature 265:137–140.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

May, R. M. 1979. Patterns in the abundance of parasites on plants. Nature 281:425–426.

O'Connor, B., W. Dritschilo, D. Nafus, and H. Cornell. 1977. Reply. Science 195:596–598.

Ohsumi, S. 1976. Population assessment of the Californian gray whale. Rep. Int. Whaling Comm. 26:250–359.

Opler, P. A. 1974. Oaks as evolutionary islands for leaf-mining insects. Am. Sci. 62:67–73.

Reilly, S. B., D. W. Rice, and A. A. Wolman. 1980. Preliminary population estimate for the Californian Gray Whale based on Monterey Shore censuses, 1967/68 to 1978/79. Rep. Int. Whaling Comm. 30:359–368.

Rey, R. J., E. D. McCoy, and D. R. Strong, Jr. 1980. Time and species richness of phytophages. Am. Nat. 117:611–622.

Rigby, C., and J. H. Lawton. 1981. Species-area relationships of arthropods on host plants: herbivores on bracken. J. Biogeogr. 8 (in press).

Southwood, T. R. E. 1961. The number of species of insect associated with various trees. J. Anim. Ecol. 30:1–8.

———. 1977. The stability of the trophic milieu, its influence on the evolution of behaviour and of responsiveness to trophic signals. Colloq. Int. Cent. Natl. Rech. Sci. 265:471–493.

Strong, D. R., Jr. 1974. Nonasymptotic species richness models and the insects of British trees. Proc. Natl. Acad. Sci. USA 71:2766–2769.

———. 1979. Biogeographic dynamics of insect-host plant communities. Annu. Rev. Entomol. 24:89–119.

Strong, D. R., Jr., and D. A. Levin. 1979. Species richness of plant parasites and growth form of their hosts. Am. Nat. 114:1–22.

Ward, L. K. 1977. The conservation of juniper: the associated fauna with special reference to Southern England. J. Appl. Ecol. 14:81–120.

Winter, T. G. 1974. New host plant records of Lepidoptera associated with conifer aforestation in Britain. Entomol. Gaz. 25:247–258.

Zimushko, V. V., and M. V. Ioashin. 1980. Some results of Soviet investigations and whaling of gray whales (*Eschrichtius robustus*, Lilljeborg, 1961). Rep. Int. Whaling Comm. 30:237–246.

JOHN H. LAWTON

DEPARTMENT OF BIOLOGY
UNIVERSITY OF YORK
HESLINGTON, YORK Y01 5DD
ENGLAND

HOWARD CORNELL

SECTION OF ECOLOGY AND ORGANISMIC BIOLOGY
SCHOOL OF LIFE AND HEALTH SCIENCES
UNIVERSITY OF DELAWARE
NEWARK, DELAWARE 19711

WILLIAM DRITSCHILO

ENVIRONMENTAL SCIENCE AND ENGINEERING
UNIVERSITY OF CALIFORNIA
LOS ANGELES, CALIFORNIA 90024

STEPHEN D. HENDRIX

DEPARTMENT OF BOTANY
UNIVERSITY OF IOWA
IOWA CITY, IOWA 52242

Submitted March 13, 1980; Revised September 29, 1980; Accepted October 16, 1980.