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Ecology, Vol. 62, No. 3. (Jun., 1981), pp. 532-537.

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THE PEAK IN NORTH AMERICAN ICHNEUMONID SPECIES RICHNESS LIES BETWEEN 38° AND 42°N¹

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Abstract. An evaluation of the geographic distribution of ≈60% of the 2809 described Nearctic Ichneumonidae shows that of the species whose latitudinal ranges contact a given latitudinal band, the number per million square kilometres is greatest between latitude 37.5° and 42.4°N, with ≈900 species/10⁶ km². The most severe absolute drop in species richness occurs in moving southward from the 37.5°-39.9° band to the 35.0°-37.4° band, with virtually no change in land mass over the same latitudinal change, and the smallest drop in species richness occurs in moving from the 32.5°-34.9° band to the 30.0°-32.4° band, where the land mass is almost halved. Of species whose southern range ends in a particular latitudinal band, the number per million square kilometres is greatest for 32.5°-34.4°N and drops away gradually in both directions. These results are consistent with the hypothesis that parasitic Hymenoptera do not increase in species richness with decreasing latitude to the same degree as their hosts. Various hypotheses are discussed as to why this might occur in Ichneumonidae.

Key words: *geographic variation; Hymenoptera; Ichneumonidae; parasitoids; resource division; tropics.*

Does species richness of entomophagous parasitoids increase along the latitudinal gradient of increasing species richness of insects as a group? Evidence is accumulating to suggest that it does not (Owen and Chanter 1970, Owen and Owen 1974, Janzen and Pond 1975, Rathcke and Price 1976, Janzen 1977), but with two dissenting opinions (Hespenheide 1979, Morrison et al. 1979). The expectation that parasitoid species richness will increase when prey species richness increases (e.g., Price 1977) ignores the fact that if there are more species of prey, there must be fewer of each kind if the aggregate insect biomass or turnover rate does not increase. As the parasitoid resource base becomes ever more finely divided, there must come a point where the carrying capacity of the habitat for parasitoid species is reduced by further resource fragmentation. To see if geographic heterogeneity of parasitoid species richness is consistent with this hypothesis, I here examine the geographic distribution of North American ichneumonid wasps (Hymenoptera: Ichneumonidae).

THE ANIMALS

"The Ichneumonidae is one of the largest of all animal groups; it includes more species than the entire Vertebrata and more than any other family, with the possible exception of the Curculionidae. In parts of the world, Ichneumonidae comprise 5-8% of all insect species" (Townes 1969). In Great Britain, they make up 9.6% of the well-known insect fauna (Kloet and Hincks 1978). Ichneumonid wasps find their hosts by searching vegetation on wing or foot. They oviposit through leaf tissue, wood, cocoon walls, dirt, etc. into

or on insect larvae and pupae of a very large number of species, primarily in the Lepidoptera, Hymenoptera, Diptera, and Coleoptera. One to a few larvae develop inside the host, feeding on various tissues and eventually killing the host. The larva pupates in or outside of the host, and often in a silken cocoon of its own construction. Shortly after eclosion it mates and repeats the cycle (there are, however, parthenogenetic species). Conspicuous specializations, with resultant resource partitioning, involve ovipositor length, leg structure, body size, adult feeding behavior, type and shape of habitat searched, pupal dormancy, stage of host attacked, substrate type searched, etc. (e.g., Townes 1969, Askew 1971, P. W. Price 1972 and *personal communication*, Porter 1977). Accounts of ichneumonid biology leave one with the distinct impression that the life-form of the host, its microhabitat, and its behavior are more important in host availability to a species of ichneumonid wasp than are many of the traits used in the alpha or even beta taxonomy of the host species. All species of medium-sized sphinx moth larvae feeding on understory shrubs in a tropical deciduous forest may be hosts for a single species of large ichneumonid. It probably does not make much difference to a parasitoid of a sphinx moth larva what is passing through the caterpillar's gut or what color of stripes it has. Porter (1977) noted of Texas mesostenine ichneumonids that "most species are taxonomically catholic in host selection, each one being attracted to diverse kinds of pupae in a restricted spatial niche (leaf rolls, ground litter, stems, tunnels, in tree trunks, etc.) rather than choosing victims from among one particular genus or even family of insects."

In short, as the species richness of ichneumonid hosts increases beyond low levels, it should not produce more kinds of resources of the type that allow

¹ Manuscript received 28 January 1980; revised 15 September 1980; accepted 17 September 1980.

TABLE 1. Number of ichneumonid species whose distributions contact a particular latitudinal band in North America north of Mexico.

Degrees north latitude	Banchinae	Lissonotini	Banchini	Mesochorinae	Gelinae	Hemigasterini	Mesostenini	Diplazontinae	Metopiinae	Ephialtinae	Xoridinae	Acaenitinae	Sum for eight sub-families	Area (km ²)	Species richness/10 ⁶ km ²
70.0-72.5	4	2	2	1	4	4	0	4	0	0	0	0	13	337 500	39
67.5-69.9	12	5	7	3	23	14	9	16	0	2	0	0	56	893 750	63
65.0-67.4	30	14	16	11	28	15	13	27	0	16	1	1	114	1 098 280	104
62.5-64.9	50	23	27	24	41	22	19	59	8	33	2	2	199	1 045 000	190
60.0-62.4	71	35	36	32	60	37	23	67	11	43	4	2	290	1 118 910	259
57.5-59.9	100	48	52	35	59	32	27	66	13	48	3	2	326	968 520	337
55.0-57.4	108	48	60	41	61	34	27	69	13	49	3	2	346	1 031 250	336
52.5-54.9	144	59	85	58	108	52	56	72	36	70	4	4	496	1 295 310	383
50.0-52.4	186	71	115	61	145	59	86	80	49	88	15	8	632	1 276 170	495
47.5-49.9	263	99	164	69	199	85	114	81	63	115	30	12	832	1 227 190	678
45.0-47.4	293	112	181	77	259	110	149	85	93	137	35	13	992	1 221 880	812
42.5-44.9	315	122	193	81	287	116	171	80	100	139	38	16	1056	1 240 500	851
40.0-42.4	316	117	199	84	293	108	185	81	110	144	39	15	1082	1 203 830	899
37.5-39.9	318	121	197	84	275	75	200	65	105	139	42	11	1039	1 155 840	899
35.0-37.4	250	93	157	59	231	55	176	41	81	117	37	8	824	1 131 370	728
32.5-34.9	196	71	125	37	172	27	145	24	58	93	28	4	612	1 032 980	593
30.0-32.4	124	53	71	21	94	2	92	13	21	48	17	2	340	651 950	522
27.5-29.9	42	14	28	13	69	1	68	12	12	37	12	0	197	541 010	364
25.0-27.4	27	9	18	9	43	0	43	11	2	21	5	0	118	433 600	272
Mexico	5	5	10	6	21	0	21	11	1	13	2	0	69		

for stacking of ever more species of ichneumonids into a habitat. Those new distinctive resource types that appear with increasing host species richness are likely to be ever smaller bits of resource, and therefore ever less likely to support a specialist ichneumonid. Furthermore, such distinctive new resource types as appear during increasing host species richness should lower the overall carrying capacity of the habitat for ichneumonids when they are too small for a specialist and too different for a generalist ichneumonid to use.

THE DATA

The persistent and long-term attention given to the Ichneumonidae of the world by Henry and Majorie Townes and by fellow ichneumonid enthusiasts has resulted in an organized compilation of the distributions of $\approx 60\%$ of the estimated 2809 valid Nearctic species names of Ichneumonidae (Townes 1969). Of the 25 subfamilies of Ichneumonidae, eight have been thoroughly catalogued for North America north of Mexico (Metopiinae, Townes and Townes 1959; Ephialtinae, Xoridinae and Acaenitinae, Townes and Townes 1960; Gelinae, Townes and Gupta 1962, Townes and Townes 1962; Diplazontinae, Dasch 1964; Mesochorinae, Dasch 1971; Banchinae, Townes and Townes 1978). These eight contain 120 of the ≈ 450 ichneumonid genera found in this area and the cataloguing is not believed to be biased toward either tropical or extra-tropical groups (H. Townes, *personal communication*).

For each of the 1717 species discussed in the eight subfamily accounts, I recorded the latitudinal range

from the subfamily catalogues listed above. All subspecies of a species were pooled to form one species entry. Records for Greenland were ignored. There is no reason to believe that ichneumonid collecting in North America over the last century was sufficiently different from that of other insects to introduce strong artificial heterogeneity into the distributional data.

Beginning with latitude 25°N, North America was divided into bands of 2.5° width. The most northerly and most southerly bands in which a species had been recorded were taken to indicate the limits of the species' latitudinal range, and the species was considered to occur in all bands between these limits. Land surface areas of the latitudinal bands were calculated from atlases. They include large freshwater bodies since no inland water body exceeded 10% of the area of a latitudinal band.

RESULTS

Of the described ichneumonid species whose latitudinal ranges contact a given latitudinal band, the number per million square kilometres is greatest between latitude 37.5° and 42.4°N, with ≈ 900 species/10⁶ km² for this latitude (Table 1). In short, the greatest species richness of ichneumonids is found from central Virginia and Kentucky to central New York on the east coast, from southern Missouri to northern Iowa in the central United States, and from central California to southern Oregon on the west coast. Moving north from this band, ichneumonid species richness drops off gradually but even as far north as 55°-60° (central Manitoba to southern Northwest Territories and Alas-

TABLE 2. Number of ichneumonid species whose southernmost distributional record occurs in a particular latitudinal band in North America north of Mexico.

Degrees north latitude	Banchinae	Lissonotini	Banchini	Mesochorinae	Gelinae	Hemigasterini	Mesostenini	Diplazontinae	Metopiinae	Ephialtinae	Xoridinae	Acaenitinae	Sum for eight sub-families	Species richness/10 ⁶ km ²	Percent of species gone at southern limit
70.0–72.5	0	0	0	0	0	0	0	1	0	0	0	0	1	0.3	0
67.5–69.9	0	0	0	0	1	1	0	0	0	0	0	0	1	1.1	0.1
65.0–67.4	2	1	1	0	1	0	1	0	0	0	0	1	4	3.6	0.4
62.5–64.9	4	2	2	0	3	1	2	3	1	1	0	0	12	11.5	1.1
60.0–62.4	3	1	2	3	9	8	1	3	0	0	0	0	18	16.1	2.1
57.5–59.9	13	7	6	2	3	2	1	1	0	2	1	0	22	22.7	3.4
55.0–57.4	3	2	1	0	1	1	0	1	0	0	0	0	5	4.8	3.7
52.5–54.9	6	3	3	2	2	2	0	1	0	2	0	0	13	10.0	4.4
50.0–52.4	6	3	3	2	1	0	1	2	1	1	0	0	13	10.2	5.2
47.5–49.9	17	7	10	6	3	1	2	2	1	2	2	1	34	27.7	7.2
45.0–47.4	9	4	5	4	19	12	7	6	9	4	1	2	54	44.2	10.3
42.5–44.9	41	18	23	6	28	15	13	4	9	7	5	3	103	83.0	16.3
40.0–42.4	37	14	23	12	57	37	20	18	22	15	4	5	170	141.2	26.2
37.5–39.9	98	41	57	27	72	23	49	26	34	25	9	3	294	254.3	43.3
35.0–37.4	79	31	48	24	75	30	45	17	25	32	11	4	267	236.1	58.9
32.5–34.9	117	39	78	17	91	25	60	11	39	48	13	2	338	327.2	78.6
30.0–32.4	87	41	46	9	28	1	27	1	10	16	9	2	162	248.5	88.0
27.5–29.9	18	6	12	4	31	1	30	1	10	17	7	0	88	162.7	93.0
25.0–27.8	12	4	8	3	22	0	22	0	1	8	3	0	49	112.9	96.0
Mexico	15	5	10	6	21	0	21	11	1	13	2	0	69		
													Σ = 1717		

ka) there are still ≈ 300 species/10⁶ km². Moving south from the peak of species richness, the number of species per square kilometre likewise declines, but at a faster rate. It is particularly striking that the most severe absolute drop occurs at $\approx 37.5^\circ$ and with virtually no change in land mass within the latitudinal band, and that the smallest step in this decline in species richness occurs at 32.5° where the land mass is almost halved.

These patterns, and the ones that are described below, are not due to exceptional behavior by any one subfamily of ichneumonids, as can be seen by inspection of Tables 1, 2, and 3.

Of ichneumonid species whose southern range ends in a particular latitudinal band, the number per million square kilometres is greatest for the band 32.5°–34.4°N (South Carolina–southern Arkansas–southern California), and drops away gradually in both directions but at a slightly slower rate to the north (Table 2). There also is a distinct small peak at 57.5°–59.9°N (northern British Columbia–Manitoba–Quebec). The percent of species that have disappeared by the time a given latitude is reached (moving south) gradually increases at an increasing rate until 32.5°–34.4°N, and then the rate of increase drops off rapidly (Table 2).

Of species whose northern ranges end in a particular latitudinal band, the pattern of numbers per square kilometre is more difficult to describe (Table 3) than the two other patterns. Starting in the north, it rises and falls irregularly until 30°N, and then abruptly drops off. In short, species that terminate their ranges

north of the arctic circle are more numerous per square kilometre than are those in the Florida–south Texas region. The area where the most latitudinal ranges have their northern limit is the band of 47.5°–49.9°N (roughly along the western United States–Canada border and southern Ontario and Quebec).

DISCUSSION

It is obvious that there is not a uniformly increasing gradient in ichneumonid species richness with decreasing latitude down North America north of Mexico. There is something about the biology of Ichneumonidae that results in highest species richness per unit area at a decidedly extra-tropical latitude, at least for latitudes north of 25°. There are two habitat traits that should be considered in determining the intensity of species packing by Ichneumonidae (as well as other parasitoids). One is the number of kinds of hosts and the other is the average (or perhaps modal) host population size. I have argued elsewhere (Janzen and Pond 1975, Janzen 1977) that since species richness of insects in general increases with decreasing latitude, the average host population size must decline over this gradient. No data suggest that the standing crop of insects or turnover rate during the growing season increases with decreasing latitude. At far northern latitudes the host resource is probably so poorly subdivided for ichneumonids that interspecific competitive interactions interfere with species packing. Moving south to the mid-latitudes, the increasing number of kinds of hosts should allow for more coexisting ich-

TABLE 3. Number of ichneumonid species whose northernmost distributions contact a particular latitudinal band in North America north of Mexico.

Degrees north latitude	Banchinae	Lissonotini	Banchini	Mesochorinae	Gelinae	Hemigasterini	Mesostenini	Diplazontinae	Metopiinae	Ephialtinae	Xoridinae	Acaenitinae	Sum for eight sub-families	Species richness/10 ⁶ km ²
70.0–72.5	4	2	2	1	4	4	0	4	0	0	0	0	13	38.5
67.5–69.9	8	3	5	2	19	10	9	13	0	2	0	0	44	49.2
65.0–67.4	18	9	9	8	6	2	4	11	0	14	1	1	59	53.7
62.5–64.9	22	10	12	13	14	7	7	32	8	17	1	1	109	104.3
60.0–62.4	25	14	11	8	22	16	6	11	4	11	2	1	84	75.1
57.5–59.9	32	14	18	6	8	3	5	2	2	5	0	0	55	56.8
55.0–57.4	21	7	14	8	5	4	1	4	0	3	0	0	41	39.8
52.5–54.9	39	13	26	17	48	19	29	4	23	21	1	2	155	119.7
50.0–52.4	48	15	33	5	39	9	30	9	13	20	11	4	149	116.9
47.5–49.9	83	31	52	10	55	26	29	3	15	28	15	4	213	173.6
45.0–47.4	47	20	27	14	63	26	37	6	31	24	7	2	194	158.8
42.5–44.9	31	14	17	8	47	18	29	1	16	6	5	4	118	95.1
40.0–42.4	42	13	29	8	34	7	27	5	19	12	6	2	128	106.3
37.5–39.9	39	18	21	12	39	4	35	2	17	10	7	1	127	109.9
35.0–37.4	30	13	17	2	28	3	25	2	10	3	4	0	79	69.8
32.5–34.9	25	9	16	2	16	2	14	0	2	8	2	0	55	53.2
30.0–32.4	45	21	24	1	13	0	13	0	2	3	2	0	66	101.2
27.5–29.9	5	2	3	1	3	0	3	0	1	5	4	0	19	29.1
25.0–27.4	3	1	2	0	5	0	5	0	0	1	0	0	9	20.8
													Σ =	1717

neumonids; however, proceeding into more tropical latitudes there should appear a point where host population densities are so low that they begin to be a barrier to wasp species richness by rendering certain host species too scarce to serve as a specialist's host. The surviving wasps will have to be either more polyphagous on an even more diverse set of hosts or better at finding scarce hosts; both challenges should slow or even reverse the rate of climb of ichneumonid species density with further increases in host species richness. The data in Tables 1–3 suggest that if this is occurring, the breakpoint falls between latitude 37.5° and 42.4°N in North America. R. R. Askew (*personal communication*) notes that Pteromalidae in Europe/Africa seem to have a distribution pattern similar to that described here for ichneumonids. I hypothesize that it is for the same reasons.

No data are available that allow a comparison between the patterns of ichneumonid species richness in Tables 1–3 with those of insects in general. However, it is certainly true that beetles and Lepidoptera, two of the major host orders for Ichneumonidae, do not have a peak in species richness in the central latitudes of the United States with a decline from there south. Great Britain provides an instructive comparison. With an area of 217 990 km², Britain has an ichneumonid species richness of ≈9303 species/10⁶ km² (total ichneumonid fauna of 2028 species, Kloet and Hincks 1978). Townes (1969) estimated that ≈35% of the Nearctic ichneumonids have been described. The maximum density of species reported in Table 1 is 899 species/10⁶ km². Table 1 is based on 60% of the

described species in North America (Townes 1969). The maximum density of described species is therefore 1498 species/10⁶ km². This is 35% of 4280. Great Britain, while spanning 50°–59°N and being an island, therefore has 2.17 times the ichneumonid species richness of the most species-rich part of North America north of Mexico. Britain does not have even close to 2.17 times the species richness of any of the larger host orders at their points of highest species richness in North America north of Mexico. The most extreme case of high ichneumonid species richness in a habitat poor in insect species is offered by H. Townes (*personal communication*). He estimates that northern Ellesmere Island (81°N) has ≈100 species of ichneumonids; he collected 30 species in 2 d.

The results in Tables 1–3 are supported by Heinrich's (1977) analysis of southeastern United States Ichneumoninae, a subfamily not included in my analyses:

“A startling feature of the Florida Ichneumoninae is the small number of forms. The 75 species and subspecies known from this state comprise little more than one-third of the ≈220 forms recorded for New England by Heinrich (1961–1962). It might seem reasonable to assume a causal relation between the scarcity of species and the late appearance of the peninsula of Florida, but I prefer an ecological, particularly climatic explanation. Globally the Ichneumoninae have proliferated in speciation only in moderate and cool climates. In the hot tropical and subtropical belt the number of species

is considerable only in the mountains. Starting with moderate numbers from $\approx 1,500$ ft [457 m] above sea level, the quantity of species increases markedly as the elevation rises to $\approx 6,000$ [1828 m] or even to 9,000 ft [2743 m], according to the presence of suitable vegetation. The tropical lowland jungles are always poorly populated by Ichneumoninae, as is true of all coastal lowlands in the tropical and subtropical belt. Florida is no exception, and it shares the comparatively small number of forms of Ichneumoninae with all neighboring states" (Heinrich 1977).

Townes (1972) has also been puzzled by the apparent paucity of Ichneumonidae in the lowland tropics and postulates that it may be due to a scarcity of early morning dew as drinking water for the wasps. While dewfall frequency and intensity are obviously heterogeneous in the lowland tropics, the Costa Rican rain forest and deciduous forest lowland habitats I work in are rich in dew or free surface moisture during the rainy season, which is the time when adult ichneumonids have the most prey available. Dew is commonplace even during the dry season in most Costa Rican lowland habitats.

D. Strong (*personal communication*) has stressed that the greater ichneumonid species richness in mid-latitudes could be in part a product of the strong peaking of density of susceptible hosts generated by winter-summer cycles. Such a peak should increase the host density at the time of parasitoid oviposition even if annual or growing-season density of hosts was the same at mid- to low latitudes. While I agree that such a phenomenon is a likely contributing factor, there are two processes that probably weaken its contribution. First, in highly pulsed host availability, the opportunity for parasitoid satiation is greatly increased. Second, in lowland deciduous tropical forests the bulk of the potential ichneumonid hosts species have a seasonal, highly pulsed peak of reproduction at the beginning of the rainy season, a pulse that closely parallels that of an extra-tropical spring.

I do not expect all groups of entomophagous parasitoids to show the same geographic species richness pattern as ichneumonids. The most extreme deviation should be displayed by egg parasitoids such as Trichogrammatidae. I suspect that insect eggs probably have the least interspecific variation, in the eyes of a parasitoid, of any host stage. Because of this, I expect egg parasitoids to increase in species richness slowly with decreasing latitude to a peak somewhere in that part of the tropics with the most complex climate and vegetation structure. Among all the types of parasitoids, I also expect egg parasitoids to have the highest proportion of very widely distributed species. One might expect pupal parasitoids to show a pattern somewhere between that envisioned for ichneumonids as a whole and for egg parasites. However, the Ich-

neumoninae analyzed by Heinrich (1977) and the Gelinae in Tables 1-3 are almost entirely parasites of pupae or stages in cocoons (P. W. Price, *personal communication*). I expect tachinid flies to show an even more extreme pattern of reduced species richness with declining latitude than do the Ichneumonidae. This is because of the very large number of species of tropical leaf rollers and miners in plant tissue that are inaccessible to the many tachinids that oviposit directly on their hosts or on the foliage they will consume. Moving up the food chain to the predators, animals that may treat many different species of prey as nothing more than little similar bags of muscle and fat, again I expect a gradient of species richness like that postulated above for the egg parasitoids. If there is no differentiation among prey individuals, then species packing has to be based on other environmental traits than what the predator eats.

Beaver (1979) independently concluded that "the bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae) are less host specific in the tropics (West Malaysian and Fijian) than in temperate regions (France and California), even though there are considerably more species present in the tropics." He attributes this to the "greater proportion of relatively non-specific xylomycetophagous species (ambrosia beetles) in the tropics and to the greater heterogeneity of tropical forests which will make host specialization more difficult." His data also support the idea that the increase in bark and ambrosia beetle species richness as one approaches the tropics is not nearly as great as is that of the hosts. Beaver's (1979) data show that there are at least three and perhaps as many as five species of beetle per tree species in California and France (vagary necessary owing to the difficulty in deciding what is a tree) while there is conspicuously less than one beetle per tree species for West Malaysia and Fiji. There may be more species of these beetles per unit area in the tropics, but there are not nearly as many as there should be if subdivision of the beetles' resource led to proportional subdivision of user populations.

To conclude, I hypothesize that increasing resource subdivision (increased species and life-form richness of parasitoid hosts) will lead to increasing species richness in a portion of the next trophic level (entomophagous parasitoids) only up to the point where further subdivision demands increased polyphagy or increased prey location efficiency owing to shrinking average host population sizes. At this point, I hypothesize that further resource subdivision will cause a decline in species richness of the next trophic level because some of its members will not be able to meet either of these demands and because some resources will then go unused by a major portion of the members of that trophic level (Janzen 1977). The available data for North American ichneumonid species richness distribution are consistent with these hypothesized pro-

cesses, but the only true test will have to be derived from natural history information not yet gathered on entomophagous parasitoids and their hosts.

ACKNOWLEDGMENTS

This study was supported by NSF grant DEB 77-04884. H. and M. Townes were extremely helpful with enthusiasm, references, and unpublished data. W. Hallwachs did the tedious job of extracting the data. H. and M. Townes, R. A. Beaver, W. Hallwachs, P. W. Price, A. M. Kuris, B. J. Rathcke, R. R. Askew, C. C. Porter, D. Strong, J. H. Lawton, and H. A. Hespeneide offered constructive comments on the manuscript. The study was made possible by H. and M. Townes' consistency in the way they mapped distributions in their various studies of Ichneumonidae.

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