

Diversity studies of salmonella incidents in some domestic livestock and their potential relevance as indicators of niche width

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SUMMARY

This study attempts to determine whether or not livestock are becoming more susceptible to epidemics of salmonella infections by the analysis of published data on the annual number of reported infections in various animals. The number of incidents reported each year may be subject to a variety of biases due to temporal and geographical differences in reporting practices. This study analysed these reports by the calculation of diversity indices which are not subject to some of these potential biases. The relationship between the ecological concept of niche width and the diversity of species or types occupying that niche is discussed. The diversity of salmonella types reported in fowl has shown a highly significant decline over the 13-year period 1976–88. It is suggested that this declining diversity may be related to the declining niche width of the biotope available to this pathogen. Although speculative, this reduction in niche width could be related to a declining genetic diversity in the host animals or to an increasing intensification of animal husbandry.

INTRODUCTION

Recent years have seen a fairly dramatic increase in the reported incidence of human salmonella infections in both the United Kingdom and the United States [1, 2]. It has been known for many years that human salmonellosis is a zoonotic infection and that the strains involved reflect those found in the domestic animal reservoir [3]. In the most recent increase of human *Salmonella enteritidis* infections, poultry appears to be the major source [1, 2, 4]. Indeed this recent increase in human infections was preceded by an equivalent increase in reported poultry infections. These findings raise the question of whether the recent trends in salmonella infections are due to changes in farming techniques.

Whether the recent outbreaks of salmonellae are related to changes in farming practice is difficult to answer by experimental methods. Similarly, monitoring reports of salmonella incidents may not give this answer as changes in reporting practices may have a greater impact on absolute numbers of reports than any underlying tendency in the general susceptibility to outbreaks of infection. One

approach, that has not yet been applied, may be to investigate the biological diversity of salmonella infections within domestic livestock. Diversity studies analyse the structure of the incidence data rather than the absolute incidences themselves, so reducing the effect of bias due to differences in reporting practices.

The investigation of biological diversity is a branch of biometry with particular application to statistical ecology [5, 6]. Studies of biological diversity occupy a pivotal position in ecological theory as they relate to resource partitioning between competing species and the powerful niche theory [6, 7]. In particular, biological diversity is expected to be greater in habitats with wide ecological niches [7–9]. As yet only a few studies have used diversity indices to investigate biological diversity in microbial populations [10, 11].

One explanation of the recent increase in the incidence of salmonella infections in man and his food animals may be that decreasing diversity of the genetic base of certain domestic livestock and in their handling has led to a reduction in niche width for pathogenic bacteria. If this is the case then it should be expected that well adapted pathogens would best be able to exploit that niche, with a resulting decline in the diversity of the pathogenic bacteria [12, 13]. This paper attempts to determine whether the niche width in domestic livestock is decreasing by the analysis of any decrease in the diversity in reports of salmonella incidents in the United Kingdom.

MATERIALS AND METHODS

In the United Kingdom, since the Zoonosis Order of 1975, all salmonella incidents in food animals have to be reported to the Ministry of Agriculture, Fisheries and Food (MAFF). An incident is defined as 'the isolation of a salmonella from an individual animal, from a group of animals which can be identified or from their products or surroundings'. Salmonella may be identified during routine screening of healthy animals, during the investigation of disease in animals or during the investigation of the cause of human disease outbreaks. Although it is a statutory requirement that all salmonella infections are reported, it is not known what proportion of such infections are eventually reported. These reports are collated and published by MAFF every year as the number of reported incidents due to each *Salmonella* sp. for each animal type. The data used for the analysis in this paper were contained in the 1987 and 1988 reports which contain data for the years 1976–88 [14]. Reports of infection due to un-typed *Salmonella* sp. were excluded from this analysis as these may have represented several species. As the number of un-typed salmonellae was usually small in relation to the total number of reported incidents, their exclusion will not have a major impact on the diversity indices (Tables 1–5). Tables 1–5 show the total number of incidents, and the number of different types reported per animal species over the 12 years covered by the report. The data for game birds and ducks and geese were excluded as the number of reports per year was small.

The mathematical concept of biological diversity does not necessarily equate exactly with the intuitive concept of diversity. Rather biological diversity reflects the relative concentrations of different types within a population. In these analyses, two diversity indices, drawn from Hurlbert's $s(m)$ diversity index family, were used. These diversity indices can be conceptualized as the mean number of

Table 1. Annual number of reported salmonella incidents in cattle

	Year													
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	
Total number of reports	1784	1164	1427	1436	1374	1484	1618	1962	1763	1871	1553	1399	1417	
Proportion (%) not typed	6.5	2.9	3.5	2.8	2.3	1.7	0.9	0.6	2.0	1.0	2.0	2.5	2.6	
Total number typed	1668	1130	1377	1396	1343	1459	1603	1950	1728	1853	1522	1364	1380	
Number of types reported	45	43	37	36	31	46	43	48	36	37	34	38	34	
Proportion (%) of typed reports due to														
<i>S. typhimurium</i>	48.1	40.5	49.7	52.4	52.7	57.9	54.7	62.3	67.9	65.2	62.7	49.8	48.0	
<i>S. dublin</i>	40.8	44.9	40.7	40.5	37.1	29.8	34.7	30.1	24.5	27.6	30.4	39.9	44.6	
<i>S. virchow</i>	0.6	0.5	1.7	1.0	1.7	2.3	1.2	1.4	0.9	0.5	0.3	0.1	0.1	
<i>S. montevideo</i>	0.7	0.7	0.7	0.4	0.7	0.5	0.9	0.8	0.8	0.8	0.5	0.7	0.7	
<i>S. anatum</i>	1.3	2.8	0.4	0.3	0.2	0	0.1	0.2	0.3	0.6	0.5	0.7	0.3	

Table 2. Annual number of reported salmonella incidents in sheep

	Year												
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Total number of reports	44	55	58	89	98	86	193	143	149	159	153	188	189
Proportion (%) not typed	9.1	3.6	6.9	7.9	0	1.2	0.5	0.7	2.7	0	3.3	4.8	3.2
Total number typed	40	53	54	82	78	85	192	142	145	159	148	179	183
Number of types reported	16	17	14	18	16	20	23	25	19	25	25	24	22
Proportion (%) of typed reports due to													
<i>S. typhimurium</i>	30.0	22.6	31.5	26.8	21.4	29.4	30.2	35.9	40.0	33.3	32.4	19.6	15.8
<i>S. montevideo</i>	12.5	13.2	20.4	23.2	27.6	9.4	26.0	9.2	20.0	22.0	12.2	20.7	20.8
<i>S. dublin</i>	7.5	28.3	20.4	14.6	17.3	17.6	13.0	12.0	8.3	6.9	10.8	15.6	26.2
<i>S. arizonae</i>	7.5	7.5	9.3	7.3	14.3	14.1	6.8	9.9	11.0	10.1	10.8	13.4	15.3
<i>S. indiana</i>	5.0	0	1.9	1.2	0	1.2	6.3	8.5	4.1	4.4	7.4	4.5	1.1

Table 3. Annual number of reported salmonella incidents in pigs

	Year												
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Total number of reports	114	89	112	122	143	126	159	185	167	158	159	123	100
Proportion (%) not typed	16.7	7.9	21.4	7.4	4.9	3.2	0.6	1.6	4.2	3.2	1.9	8.9	2.0
Total number typed	95	82	88	113	136	122	158	182	160	153	156	112	98
Number of types reported	25	29	27	31	27	26	31	35	36	27	29	26	30
Proportion (%) of typed reports due to													
<i>S. typhimurium</i>	18.9	18.3	15.9	23.0	23.5	27.0	24.7	24.7	31.3	31.4	35.3	31.3	34.7
<i>S. derby</i>	11.6	8.5	17.0	14.2	32.4	21.3	17.1	19.8	18.8	21.6	17.9	25.0	18.4
<i>S. kedougou</i>	8.4	0	3.4	5.3	3.7	7.4	6.3	8.2	6.9	7.2	5.8	6.3	4.1
<i>S. cholerae-suis</i>	14.7	15.9	10.2	4.4	2.2	2.5	2.5	1.6	1.3	3.3	0	0	1.0
<i>S. give</i>	1.1	9.8	2.3	6.2	5.9	2.5	1.9	1.1	2.5	5.2	5.8	1.8	4.1

Table 4. Annual number of reported salmonella incidents in fowl

	Year												
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Total number of reports	522	446	879	1079	1433	732	616	514	446	456	519	497	838
Proportion (%) not typed	16.3	4.3	10.8	11.6	13.1	9.6	6.0	4.3	1.6	1.8	1.4	1.8	4.3
Total number typed	439	427	784	954	1245	662	579	492	439	448	512	488	802
Number of types reported	43	42	50	47	49	47	42	38	33	44	37	36	35
Proportion (%) of typed reports due to													
<i>S. typhimurium</i>	15.0	8.7	14.0	12.2	14.1	12.0	10.0	18.7	30.8	21.4	25.4	18.9	9.7
<i>S. seftenberg</i>	6.4	7.2	5.4	10.2	20.2	20.6	24.5	22.2	12.1	18.3	9.8	8.2	6.0
<i>S. montevideo</i>	3.0	1.6	8.9	7.5	9.2	14.8	14.7	10.2	10.0	7.1	5.3	2.9	4.4
<i>S. enteritidis</i>	3.0	1.6	2.6	1.0	0.6	1.2	1.4	0.2	0	3.3	7.0	22.7	50.0
<i>S. agona</i>	20.5	9.8	8.9	7.8	8.0	4.0	6.0	2.6	2.5	4.2	2.3	0.6	0.4

Table 5. Annual number of reported salmonella incidents in turkeys

	Year												
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Total number of reports	138	135	262	231	264	256	151	133	122	79	233	107	212
Proportion (%) not typed	13.0	4.4	6.9	6.5	17.4	20.7	4.0	4.5	6.6	2.5	1.3	1.9	2.4
Total number typed	120	129	244	216	218	203	145	127	114	77	230	105	207
Number of types reported	21	26	24	30	29	29	14	19	26	27	28	19	27
Proportion (%) of typed reports due to													
<i>S. hadar</i>	32.5	34.1	39.3	43.5	32.1	25.6	30.3	18.9	18.4	7.8	9.6	9.5	6.2
<i>S. heidelberg</i>	7.5	17.8	5.3	9.3	4.6	0.5	30.3	19.7	22.8	6.5	10.9	2.9	5.8
<i>S. agona</i>	12.5	8.5	10.7	12.5	11.5	1.5	10.3	9.4	7.0	6.5	6.5	8.6	6.3
<i>S. seftenberg</i>	8.3	3.1	3.7	3.2	1.8	7.9	8.3	6.3	6.1	7.8	5.7	13.3	10.1
<i>S. newport</i>	0	0	0.8	0.9	0.9	1.5	0	19.7	5.3	15.6	6.5	17.1	11.1

represented categories in a random sample of size m sampled repeatedly in a large series. The index equation for this family is

$$s(m) = \sum_{i=1}^S (1 - (1 - p_i)^m) \quad (m = 2, 3, \dots),$$

where S is the number of non-empty categories, p_i is the probability of sampling a member of the i th categories and m is a, an integer determined by the investigator [15, 16]. Following previous studies, $m = 2$ was chosen to give more weight to the most common categories and $m = 50$ chosen to give increased weight to less common categories [16–18].

As the data are in fact a sample, rather than the total population of salmonella infections, the following estimation of $s(m)$ was calculated:

$$\hat{s}(m) = \sum_{i=1}^S (1 - \binom{n-n_i}{m} / \binom{n}{m}) \quad (n \geq m),$$

where n_i is the frequency of the i th category and n is the sum of the n_i s for all categories. Note that ${}^a C_k$ denotes the binomial coefficient. The general definition for the binomial coefficient for any real or complex a and non-negative integer k is given by [19]

$${}^a C_k = \frac{a(a-1)(a-2)\dots(a-k+1)}{k!}.$$

In fact $\hat{s}(m)$ is the minimum variance unbiased estimate of $s(m)$, if we consider (n_1, \dots, n_s) as a sample from the polinomial universe (p_1, \dots, p_s) .

For example, if we take a population of 50 individuals divided into 4 groups, the 4 groups containing 20, 15, 10 and 5 members each $\hat{s}(2)$ would be calculated as follows:

$$\begin{aligned} \hat{s}(2) &= \left(1 - \left[\frac{{}^{50-20}C_2}{{}^{50}C_2}\right]\right) + \left(1 - \left[\frac{{}^{50-15}C_2}{{}^{50}C_2}\right]\right) + \left(1 - \left[\frac{{}^{50-10}C_2}{{}^{50}C_2}\right]\right) + \left(1 - \left[\frac{{}^{50-5}C_2}{{}^{50}C_2}\right]\right) \\ &= 4 - \frac{1}{(50 \times 49)/2} \left(\frac{30 \times 29}{2} + \frac{35 \times 34}{2} + \frac{40 \times 39}{2} + \frac{45 \times 44}{2}\right) = 1.7143 \end{aligned}$$

This is the unbiased estimate of $s(2)$ belonging to a theoretical population, from which the above 50 individuals have been sampled. On the other hand, 1.7143 is the exact $\hat{s}(m)$ value of the multinomial population with the probability vector

$$\left(\frac{20}{50}, \frac{15}{50}, \frac{10}{50}, \frac{5}{50}\right).$$

RESULTS

The annual proportions of the five commonest *salmonellae* for each animal are shown in Tables 1–5. The estimates of the diversity index values for the data are given in Tables 6 and 7. One of the values for the $\hat{s}(50)$ estimations are not given as the total number of reports in a year was less than 50. Most of the domestic animals have a similar diversity of salmonella carriage with the exception of cattle

Table 6. $\hat{s}(2)$ diversity indices for year and animal

	Years												
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Cattle	1.60	1.63	1.59	1.56	1.58	1.58	1.58	1.52	1.48	1.50	1.51	1.59	1.57
Sheep	1.89	1.85	1.84	1.85	1.80	1.85	1.82	1.83	1.78	1.82	1.85	1.87	1.84
Pigs	1.92	1.92	1.92	1.91	1.83	1.87	1.90	1.89	1.86	1.85	1.83	1.84	1.84
Fowls	1.92	1.95	1.93	1.94	1.90	1.91	1.89	1.89	1.86	1.90	1.90	1.88	1.72
Turkeys	1.85	1.84	1.81	1.78	1.85	1.88	1.79	1.87	1.89	1.95	1.92	1.90	1.90

Table 7. $\hat{s}(50)$ diversity indices for year and animal

	Years												
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Cattle	6.91	7.94	6.22	5.27	6.41	7.28	6.79	5.46	5.45	5.34	5.25	6.67	5.35
Sheep	—	16.37	12.88	14.20	12.61	15.18	12.24	14.89	11.50	13.82	14.91	13.35	11.61
Pigs	19.59	21.50	19.74	21.09	16.85	17.13	19.53	19.25	19.91	16.72	15.87	16.95	19.42
Fowls	20.45	21.48	19.19	19.61	15.86	18.21	16.81	16.59	14.40	17.62	16.95	15.32	11.70
Turkeys	14.31	16.40	13.26	14.71	15.84	16.84	8.93	12.45	17.17	22.48	17.13	14.53	16.33

Table 8. Regression analysis of diversity indices for animals against time*

Animal	$\hat{s}(2)$			$\hat{s}(50)$		
	b †	F ‡	p	b	F	p
Cattle	-0.0063	4.7456	0.0520	-0.127	4.815	0.0506
Sheep	-0.0017	0.6244	0.4461	-0.159	1.637	0.2296
Pigs	-0.0074	19.1838	0.0011	-0.242	4.118	0.0673
Fowls	-0.0104	11.0476	0.0068	-0.565	24.747	0.0004
Turkeys	0.0089	9.8594	0.0094	0.219	0.878	0.3689

* Data analysed by Unistat-III statistical package.

† As in the $a + bt$ linear regression line.

‡ The variance ratio F is tested on 1 and 11 degrees of freedom for all except the $\hat{s}(50)$ data for sheep which is tested on 1 and 10 degrees of freedom.

which had a rather low diversity due to the major preponderance of *S. typhimurium* and *S. dublin*. It can be seen that, with the exception of turkeys, there is a decreasing diversity of salmonella incidents over the 13 years, particularly evident in fowl. Table 8 shows the results of regression analysis of the annual changes in diversity by both $\hat{s}(2)$ and $\hat{s}(50)$. There is a significant decline in both indices of diversity for fowl. There was also a significant decrease in $\hat{s}(2)$ for pigs and an increase in $\hat{s}(2)$ for turkeys.

DISCUSSION

As already discussed diversity indices are widely used in ecological studies, in part because of their relationship to the niche width within a biotope (the biotope is the environment inhabited by an organism along with the other organisms that share that environment). Such indices have also been used in microbial ecology [10, 20, 21]. Furthermore, it has already been pointed out that an individual human can be considered as an isolated biotope for his own microorganisms [22].

It is only recently that diversity indices have been used to analyse epidemiological data [23]. We would suggest that diversity indices have particular value in epidemiological studies. For example, a major problem in the interpretation of incidence and prevalence data is that reporting practices may vary from one area to another or with time. It can be difficult in such circumstances to determine whether the prevalence of a particular infection is increasing or whether an apparent increase is due to an increase in the general level of reporting. For this reason, methods based on structural properties of the epidemiological data are preferable, assuming that the relative differences in incidence between strains are not substantially affected by difference in reporting practices. Diversity indices are not sensitive to changes in the total numbers of reports, only to changes in the relative proportions of reported types. For example, as long as the relative proportions of types remain constant, increasing numbers of reports from 100 to 1 000 000 has only a minor effect on the calculated diversity indices.

Because of their independence from the total number of reports, diversity indices provide a method of determining whether the concentration of specific diseases is changing within a community [23]. However, the indices would clearly be affected if a higher proportion of some diseases or organism types were reported than others.

A wide variety of diversity indices have been described each of which has its own particular properties [24]. The two indices, used in this study, were drawn from Hurlbert's $s(m)$ diversity index family for reasons already mentioned. These related indices can either stress the common strains, $\hat{s}(2)$, or be sensitive to changes in the less common strains, $\hat{s}(50)$. For the analysis of sample data, a unbiased estimate of the true population $s(m)$ exists [16]. These indices are also conceptually easy to comprehend, in terms of the expected number of strain types in a sample. Although not reported, the diversity indices were also calculated using N_1 from Hill's index family [25] and found to be very similar to the $\hat{s}(2)$ data.

This is the first study to report the use of diversity indices to demonstrate declining diversity of a microbial pathogen. Although the indices are not sensitive to reporting biases that result in a general under-reporting of infections, they are sensitive to those biases that result in certain types of salmonellae being reported more frequently than others.

It is notable that the only animal species that showed a consistent decline in both the $\hat{s}(2)$ and $\hat{s}(50)$ values were fowl. As discussed, fowl have been the major implicated domestic livestock in the recent epidemic of *S. enteritidis*. That the decline in diversity of salmonella types in fowl is not due to the increasing predominance of a single epidemic strain can be seen in Table 4 and Figure 1. The diversity of salmonella types in fowl has been declining whilst the reported prevalence of individual types has increased and declined. This is supported by the relatively greater decline in the $\hat{s}(50)$ index which, as discussed, tends to emphasise the less frequent categories.

We would suggest that the declining diversity of salmonella types in fowl may be related primarily to a reduction in the niche width of the biotope available to the salmonellae colonising these animals. How the niche width of this biotope has become narrowed is open to debate, but may be due to increasing intensification

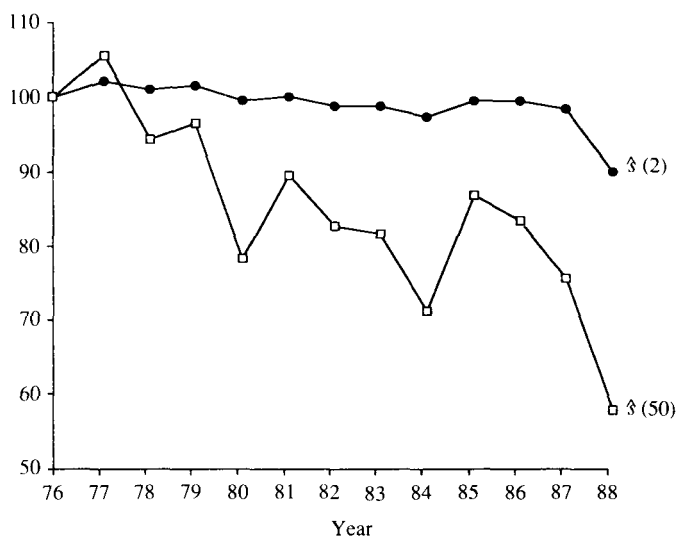


Fig. 1. Relative decline in the $\hat{s}(2)$ and $\hat{s}(50)$ diversity indices of salmonella reports in fowl.

of handling practices, reduction in the genetic diversity of the breeding stock or increasing standardisation of food type. It may not be a coincidence that, in British farming practice, fowl are particularly intensively reared. Interestingly, reduction of the diversity of death causes in humans have been described which could also be explained by narrowing of niche width as a consequence of increasing civilization [23, 26].

The lower diversity of reported salmonella incidents in cattle suggests that the ecological niche available to salmonellae in cattle is much narrower than in other livestock. This may, at first sight, appear at odds with the relatively less intense farming practices for cattle. However, the available biotope on a host animal is probably subject to factors other than farming practices and so comparisons between species should be made with care.

In conclusion, reduction in niche width of a biotope can have a dramatic effect on its resident population. A particularly well adapted species can easily overcome competing species in such a biotope and increase in population size potentially leading to an epidemic [27]. Decreasing diversity of handling practices or of the genetic stock of commercial fowl may be one of the underlying factors in the current epidemic of *S. enteritidis*. This hypothesis should be investigated further using more exact data.

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