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THE NATURAL HISTORY OF SALMONELLAE IN MAMMALS OF THE TROPICAL KIMBERLEY REGION, WESTERN AUSTRALIA

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Abstract—Screening for salmonellae was conducted on five occasions within a year on mammals from many different habitats in the Mitchell Plateau area of the tropical Kimberley Division of Western Australia. Some data were obtained from reptiles. Forty-two *Salmonella* serotypes, two *Edwardsiella* and one *Arizona* strain were isolated. Marsupials harbour significantly more (1.6 times) *Salmonella* serotypes than eutherians. Eleven *Salmonella* serotypes and one *Arizona* strain were isolated from reptiles. All *Salmonella* strains were common to the mammalian species. Varanid lizards showed higher prevalence of salmonellae than other reptilian families. Top carnivores (reptile and marsupial) show relatively high numbers of *Salmonella* serotypes and prevalence levels.

Four mammalian species showed marked seasonal variation in the prevalence of salmonellae and three species in the number of serotypes isolated. Pooled mammalian community data for individual survey sites showed similar seasonal variation which reflected the pattern seen in the predominant host species on the site. Significant seasonal variation in the prevalence of salmonella was concurrent in three of the host species showing maximum prevalence in the wet season (January–summer) followed by a declining prevalence to the end of the dry season (October). Prevalence in the fourth species was also high in January, but continued to increase after the wet season (April) before decreasing as the dry season progressed (July and October).

Dendrograms of association showed that the salmonella 'community' does not associate according to any systematic category of the hosts and no evidence of such communities was found using other criteria, such as site or coastal vs inland locations. No evidence was found for host or site specificity of given serotypes. Multiple serotype infections by salmonella were common, with up to three present in mammals and reptiles, and they occurred at random. When hosts in coastal habitats were compared with those in inland sites higher, lower or no difference was found in the prevalence of salmonella, depending upon which host was considered. Sites with similar mammals and vegetation sometimes showed marked differences in salmonella prevalence at a given time. Generally a given *Salmonella* serotype was lost from the host within ≃3 months. Surveys for salmonellae should be designed to include a range of species, replicated vegetation types and, especially, be repeated in several seasons. *Edwardsiella tarda* was isolated twice from a carnivorous marsupial.

In a discussion of unexplored areas in epidemiological studies of zoonoses, Muul [1] emphasized the need to consider aspects of the host ecology which may predispose its involvement with pathogens. He suggested several areas of importance: changes in host numbers, their distribution in space and time, feeding habits, behaviour and physiological condition. Studies of salmonella infections in wild populations mostly ignore all these factors with the exception of the few studies mentioned later.

In this paper the prevalence of salmonellae in wild mammals is examined with respect to host, site, vegetation and time in a relatively pristine, tropical environment. In a later paper we intend to consider the relationship between host physiology and the prevalence of salmonellae.

This work was conducted during a study on the ecology and physiology of tropical mammals occurring in disparate habitats. Sites sampled ranged from coastal vine thickets and mangrove through plateau (300 m) vine thickets, savannah and woodland, to riparian associations and fractured sandstones; these will be detailed elsewhere. The work was conducted in the area of the Mitchell Plateau in the northern Kimberley district of Western Australia

Order of authorship is randomized. Address correspondence concerning identification of serotypes to J. B. Iveson and analysis and interpretation to W. F. Humphreys.

Table 1. *Salmonella* serotypes isolated from mammals in different parts of the Mitchell Plateau region between October 1981 and October 1982. Those marked * were isolated in November 1982

Code	Area Location and habitat	*Salmonella* serotypes	Number of individuals trapped on site
Coast			
WV	Walsh Point vine thicket 14°33′24″S, 125°50′30″E	*bahrenfeld, bleadon, chester, eastbourne, kisarawe, muenchen, ohlstedt, ord, rubislaw, uphill, urbana wandsbek, bronx**	*Dasyurus hallucatus* (14), *Isoodon macrourus* (2), *Wyulda squamicaudata* (1), *Melomys* sp. cf. *burtoni* (33), *Zyzomys argurus* (19), *Z. woodwardi* (24)
WM	Walsh Point mosaic of mangroves and open savannah 14°34′00″S, 125°50′00″E	*bahrenfeld, bootle, bronx, bukavu, chester, hvittingfoss, jangwani, kalumburu, kinondoni, muenchen, ohlstedt, oranienburg, poona, rubislaw, treforest, urbana, wandsbek, wandsworth*	*D. hallucatus* (7), *Planigale maculata* (2), *I. macrourus* (34), *Conilurus penicillatus* (19), *Melomys* sp. cf. *burtoni* (59), *Mesembriomys macrurus* (1), *Z. argurus* (25), *Z. woodwardi* (3)
Plateau			
DV	Lone Dingo vine thicket 14°35′15″S, 125°45′40″E	*adelaide, bahrenfeld, bukavu, charity, chester, eastbourne, fremantle, muenchen, ohlstedt, rubislaw, thompson, wandsbek, urbana**	*D. hallucatus* (10), *I. macrourus* (31), *Melomys* sp. cf. *burtoni* (78), *Z. argurus* (4), *Z. woodwardi* (4)
DW	Lone Dingo eucalypt woodland 14°35′15″S, 125°45′45″E	*bahrenfeld, chester, eastbourne, jangwani, meunchen, ohlstedt, rubislaw, singapore, urbana, wandsbek, wandsworth*	*D. hallucatus* (7), *I. macrourus* (22), *C. penicillatus* (1), *Melomys* sp. cf. *burtoni* (1), *M. macrurus* (5), *Pseudomys nanus* (3), *Rattus tunneyi* (4), *Z. argurus* (16), *Z. woodwardi* (1)
PW	Mixed eucalypt woodland with *Livistona* and grass 14°49′30″S, 125°49′30″E	*bootle, jangwani, ohstedt, urbana*, S.4.5.b:-	*Phascogale tapoatafa* (1), *Planigale maculata* (6), *Sminthopsis virginiae* (2), *Trichosurus arnhemensis* (2), *Leggadina* sp. cf. *lakedownensis* (1), *P. nanus* (2), *Pseudomys (sensu lato)* sp. (7), *R. tunneyi* (3), *Z. argurus* (1)

	Serotypes on plateau from non-grid trapping		
NPW	Mixed eucalypt woodland and grass on northern plateau 14°38′00″S, 125°48′15″E	*arizonae,* bukavu, chester,* jangwani, ohlstedt, zehlendorf** (*arizonae* from a reptile)	*D. hallucatus* (7), *P. maculata* (4), *I. macrourus* (16), *C. penicillatus* (1), *Leggadina* sp. cf. *lakedownensis* (1), *Pseudomys (sensu lato)* sp. (3), *R. tunneyi* (10), *Z. argurus* (1)
PS	*Melaleuca* swamp (ephemeral) 14°46′45″S, 125°49′15″E	*litchfield, rubislaw, urbana*	*S. virginiae* (2), *Melomys* sp. cf. *burtoni* (5), *P. nanus* (2), *R. tunneyi* (72)
DV/W	Ecotone along eucalypt woodland and vine thicket 14°35′10″S, 125°45′30″E	*bootle, chester*	*D. hallucatus* (5), *I. macrourus* (7), *W. squamicaudata* (1), *Melomys* sp. cf. *burtoni* (15), *M. macrurus* (2), *Z. argurus* (20), *Z. woodwardi* (10)
Scarp			
CW	Eucalypt, *Terminalia* and *Livistona* woodland with grass 14°51′18″S, 125°49′48″E	*eastbourne, muenchen, ohlstedt, rubislaw*	*P. maculata* (3), *S. virginiae* (6), *Leggadina* sp. cf. *lakedownensis* (3), *P. nanus* (1)
Riverine			
CP	Grassland and riparian woodland at base of scarp on Camp Creek 14°52′05″S, 125°49′45″E	*bootle, eastbourne, lohbruegge, muenchen, ohlstedt, rubislaw, singapore, urbana* (*ball* from a reptile)	*S. virginiae* (3), *I. macrourus* (11), *Leggadina* sp. cf. *lakedownensis* (6), *P. nanus* (34), *R. tunneyi* (3)
CC	Riparian woodland on edge of plateau at mining exploration camp on Camp Creek 14°49′15″E. 125°50′20″S	*bootle, chester* (*bahrenfeld* from a reptile)	*P. maculata* (1), *S. virginiae* (7), *Leggadina* sp. cf. *lakedownensis* (5), *Melomys* sp. cf. *burtoni* (8), *P. nanus* (12), *Pseudomys (sensu lato)* sp. (3), *Z. argurus* (10), *Z. woodwardi* (1)
Sandstone			
CS	Fractured sandstone with mosaic of spinifex, tussock grass and woodland 14°53′30″S, 125°45′00″E	*angoda, bahrenfeld, ball, bleadon, bootle, bournemouth, brisbane, bronx, bukavu, charity, eastbourne, give, havana, houten, hvittingfoss, jangwani, kinondoni, litchfield, muenchen, ohlstedt, oranienburg, orion, potsdam, rubislaw, treforest, urbana, wandsbek, chester,* poona**	*Pseudantechinus* sp. (7), *D. hallucatus* (82), *W. squamicaudata* (23), *Pseudomys delicatulas* (2), *R. tunneyi* (1), *Z. argurus* (169), *Z. woodwardi* (10)

(≃ 14°S, 125°E). The climate is typical of the wet–dry tropics with heavy summer rainfall (November–March) followed by prolonged drought for the remainder of the year.

METHODS

The programme involved about 3-week-long sampling periods on five occasions: September–October 1981, January, April, July and September 1982. A minor sampling programme was undertaken in November and December 1982 and these data are mentioned where appropriate. Otherwise all analyses refer to the main programme between October 1981 and October 1982.

Animals were trapped in live-traps of three sizes, baited with peanut paste, oats, raisins and bacon. The traps were checked each morning between 0500 and 1100. Samples were taken on the first capture of an individual on each trip. Trapped animals were transferred to a calico bag and rectal swabs made, using sterile cotton buds, obtaining a faecal sample where possible. The swabs were broken into a vial of 4 ml strontium chloride B broth [2, 3] or used to transfer faecal samples to the fluid and then discarded. The medium was designed to enrich and preserve *Salmonella* and *Edwardsiella* for several weeks without refrigeration.

On arrival in the laboratory (within 6 weeks) about 1 ml of the medium was transferred to 10 ml of fresh strontium chloride B enrichment broth. The remainder of the field sample and the freshly inocculated enrichment medium were incubated at 43°C. After 48 h both enrichment media were subcultured to deoxycholate-citrate and modified bismuth sulphite agar [2] and colonies identified biochemically and serologically. Some reptiles trapped were treated in the same manner.

On occasion control swabs were made using the standard procedure, excluding final contact with the animal, and from the calico bags and the hands of handlers. The only isolation made from these control swabs was one *Arizona* sp. from the handlers' hands, a serotype unrecorded from any other sample from the Mitchell Plateau area.

Other than where specified, statistical treatment follows the algorithms of Sokal and Rohlf [4] and Southwood [5].

Climate of the Mitchell Plateau

Meteorological data are available only since 1970. The climate epitomises the wet–dry tropics with summer rainfall and winter drought. The mean annual rainfall is 1493 mm of which 90% occurs between November and March. Mean cloud cover for this period is 5/8 and falls to 2.4/8 for the remainder of the year. The summer cloud cover results in small annual variation (1.3 times) in solar radiation (≃ 525 mWh cm^{-2} in October [6]). This compares with an annual variation of 2.8 times in the Perth area. Mean annual maximum temperature varies little, i.e. from 29.9°C in June to 36.1°C in October and November. This climatic pattern shows little annual variation except for a single record of heavy winter rain (227 mm in May 1979; 17% of the annual total).

Human factors

The Mitchell Plateau area was occupied by an aboriginal hunter–gatherer community until the early 1940s. Since the early 1970s intensive mining exploration has been conducted on the plateau itself. Feral cattle from an adjacent pastoral station intrude up the creeks to areas around grids CC, CW, PS and CP (see Results). The area lacks many of the introduced mammals (rabbits, foxes, water buffalo, goats, donkeys and European rodents) which abound elsewhere in Australia but feral cats are present. The region as a whole is little disturbed and has suffered little contact with Europeans directly or from their introduced animals and plants.

RESULTS AND DISCUSSION

Salmonella *serotypes isolated from different hosts and sites*

Forty *Salmonella* serotypes were isolated from 1033 samples taken from mammals in the main study (Appendix 1) and a further two serotypes in November 1982. Eleven serotypes, all common to the mammals, were obtained from an additional 44 reptile samples (Appendix 2). Brief site descriptions and their location are given in Table 1. Of these sites, eight were grids of 100 trap locations (120 traps) used for a long-term capture–mark–release programme (DV, DW, WV, WM, CS, CP, CW, PW). The remainder were removal sites without fixed trap locations. Hence on the eight main sites repeated samples may include the same individuals but this was rarely the case for the remaining sites. Table 1 shows the *Salmonella* serotypes isolated from samples for each site and the mammals trapped there. Table 2 shows the mammal species from which salmonella were isolated and the serotypes involved.

Table 2. *Salmonella* serotypes isolated from mammal species in the Mitchell Plateau region between October 1981 and October 1982. Those marked * were isolated only in November 1982

Host	*N*	*Salmonella* species isolated
Marsupials		
Dasyuridae		
Dasyurus hallucatus	30	*angoda, ball, bahrenfeld, bleadon, bootle, bournemouth, brisbane, bronx, bukavu, charity, chester, eastbourne, give, houten, hvittingfoss, jangwani, kisarawe, litchfield, muenchen, ohlstedt, oranienburg, ord, orion, poona,* potsdam, rubislaw, treforest, uphill, urbana, wandsbek*
Planingale maculata	4	*eastbourne, ohlstedt, oranienburg,* S.4.5.b monophasic
Sminthopsis virginiae	5	*arizonae,* bootle, chester, muenchen, rubislaw, singapore, zehlendorf**
Peramelidae		
Isoodon macrourus	21	*adelaide, arizonae,* bahrenfeld, bootle, bronx, bukavu, charity, chester, eastbourne, hvittingfoss, jangwani, kalumburu, muenchen, ohlstedt, rubislaw, singapore, thompson, urbana, wandsbek, wandsworth, zehlendorf**
Phalangeridae		
Wyulda squamicaudata	8	*bootle, bukavu, chester, eastbourne, houten, hvittingfoss, oranienburg, rubislaw*
Eutherians		
Muridae		
Conilurus penicillatus	5	*bukavu, hvittingfoss, jangwani, muenchen, ohlstedt*
Leggadina sp. cf. *lakedownensis*	4	*chester, muenchen, ohlstedt, rubislaw*
Melomys sp. cf. *burtoni*	14	*bahrenfeld, bronx, bukavu, chester, eastbourne, fremantle, jangwani, kinondoni, muenchen, ohlstedt, oranienburg, poona, urbana, wandsbek*
Pseudomys nanus	4	*bootle, litchfield, lohbruegge, urbana*
Pseudomys (sensu lato) sp.	1	*urbana*
Rattus tunneyi	5	*bootle, jangwani, rubislaw, urbana, wandsbek*
Zyzomys argurus	14	*bahrenfeld, bootle, bronx, bukavu, chester, havana, jangwani, kinondoni, litchfield,* muenchen, ohlstedt,* oranienburg, rubislaw, wandsbek*
Z. woodwardi	7	*bahrenfeld, chester, eastbourne, houten, muenchen, uphill, wandsbek*

Total number of serotypes in the region

Estimates of the total *Salmonella* serotype pool in the region were estimated using May's [7] formula to expose the hidden sector of a log-normal distribution. This method gives an expected total of 52 serotypes present on the sites examined and an estimated 77% discovery rate from our sampling.

Salmonella *serotypes per mammal species, systematic position and feeding habits*

We want to examine whether some hosts carry a wider range of *Salmonella* serotypes. Individual species of mammals carried between 0 and 29 of the 40 serotypes isolated (Table 2). However, the number of serotypes isolated is dependent on the logarithm of the number of samples taken. The equation (footnote to Table 3) was used to correct the number of serotypes per species to an indexed value which is the expected number of serotypes isolated from each species per 100 samples taken. This index value is shown in Table 3 (column B) and results in a range of between 8 and 27 serotypes per 100 samples. This index value is not used in subsequent analyses.

Eutherians harbour fewer serotypes than marsupials (Wilcoxon two-sample test: serotypes per samples $U_s = 33.5$, $P < 0.05$; index values $U_s = 37$, $P < 0.01$). Of the indexed values only one eutherian, *Leggadina* sp., falls within the marsupial range. On indexed values (considering only species from which salmonellae were isolated) marsupial species harbour 1.6 times as many serotypes as eutherians (respective means and standard errors 17.2 ± 2.5, 10.5 ± 1.0).

Within the marsupials *D. hallucatus* has 59% more serotypes (50% on raw data) than the next closest species, *I. macrourus*. *D. hallucatus* is a top carnivore eating reptiles and small mammals but it also scavenges and eats fruit. Hence it is likely to encounter a wide

Table 3. Number of *Salmonella* serotypes per mammal species in the Mitchell Plateau region between October 1981 and October 1982

Species	Number of samples	Number of serotypes	Serotypes per sample (%) A	Index * Serotypes per 100 samples B	Ascending rank order of index
Marsupials					
Pseudantechinus sp.	8	0	0	-	-
Dasyurus hallucatus	149	29	19	27	13
Phascogale tapoatafa	1	0	0	-	-
Planigale maculata	16	4	25	14	9
Sminthopsis virginiae	17	5	29	15	10
Isoodon macrourus	141	19	13	17	12
Trichosurus arnhemensis	2	0	0	-	-
Wyulda squamicaudata	37	8	22	13	8
Eutherians					
Conilurus penicillatus	31	5	16	11	6
Leggadina sp. cf. *forresti*	11	4	36	16	11
Melomys sp. cf. *burtoni*	266	14	5	9	3
Mesembriomys macrurus	2	0	0	-	-
M. gouldi	1	0	0	-	-
Pseudomys nanus	38	3	8	8	2
Pseudomys (sensu lato) sp.	10	1	10	13	7
Rattus tunneyi	46	5	11	9	4
Zyzomys argurus	201	12	6	8	1
Z. woodwardi	56	7	13	10	5
	Σ 1033				

* The number of serotypes isolated (Y) is logarithmically related to the number of samples (X) taken. For hosts with *Salmonella* isolates $Y = 12.4 \log X - 11.7$; $r^2 = 0.58$, $n = 13$, $P < 0.01$. The index is the number of serotypes isolated corrected by the slope of the above regression equation to a sample size of 100. The rank order of columns A and B is correlated (Kendalls $\gamma = 0.64$, $P < 0.01$) but the rank of *D. hallucatus*, *I. macrourus* and *Pseudomys (sensu lato)* sp. are greatly increased by use of the indexed value of the number of serotypes per host.

range of serotypes. There is no clear difference between serotype numbers present in the remaining marsupials (range 13–17) despite their widely disparate habits and habitats. *Pseudantechinus* sp., *P. tapoatafa, P. maculata* and *S. virginiae* are all carnivorous and belong to the same family (Dasyuridae) as *D. hallucatus*. At the other extreme, *T. arhnemensis* and *W. squamicaudata* are fruit and leaf eaters. Amongst the eutherians, which are all believed to be vegetarian [8], there is no clear separation of the species according to their *Salmonella* serotypes (index range 8–16 serotypes per host species).

Salmonella *serotypes from reptiles*

Samples were taken from 44 reptiles in 4 families and 21 species (Appendix 2). A total of 22 *Salmonella* isolations was made of 11 serotypes all of which were also isolated from mammals. The varanids feed on vertebrates and invertebrates, while members of the other families primarily eat invertebrates. The varanids have a higher prevalence than all other families (G-statistic, $P < 0.001$). The rank order of isolations per serotype for varanids does not differ from that for the mammals over the entire year ($U_{s10,10} = 53$, N.S.) or between mammals and varanids in May when the varanid samples were taken ($U_{s7,7} = 26$, N.S.).

Although the prevalence of salmonella infection is high in varanids and low in skinks, there is no evidence that reptiles differ from mammals in the serotypes they host or that they harbour serotypes in different proportions.

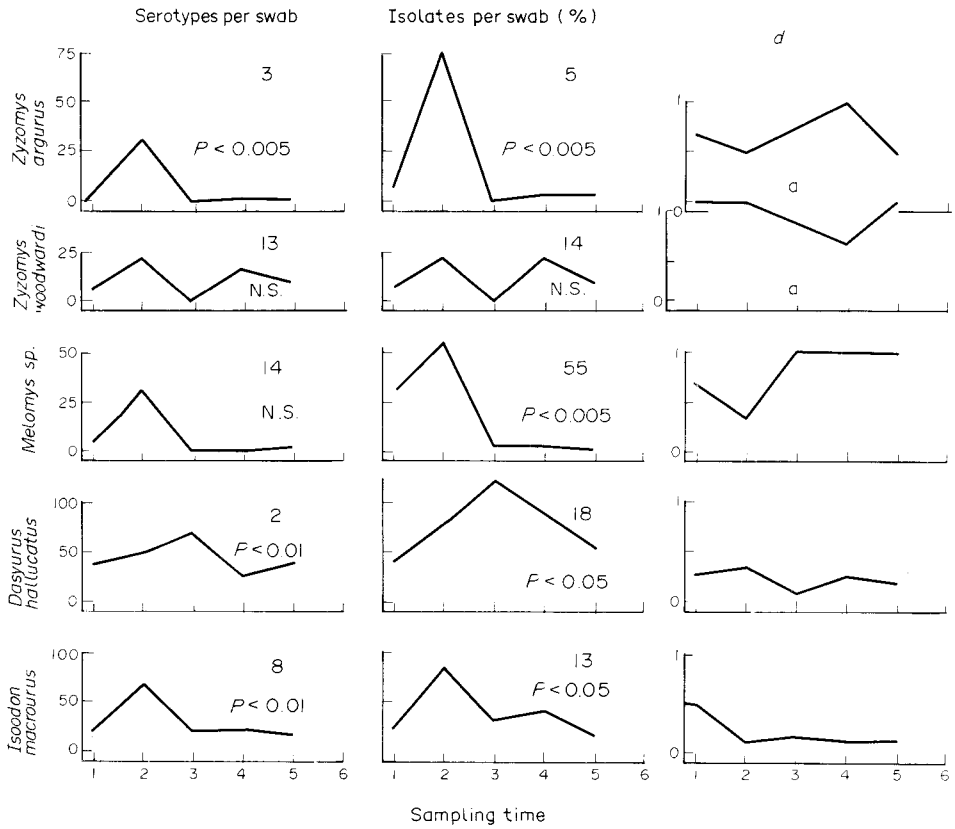

Fig. 1. The occurrence of *Salmonella* over one year in some mammal species in the Mitchell Plateau area. Mammal species considered are those from which >50 samples were taken. They are discussed in the text. Left column = serotypes per sample (%); middle column = isolates per sample (%); right column = Berger–Parker Dominance Index, $d = N_{max}/NT$, where d is the proportion of the total catch that is due to the dominant serotype. Significant seasonal variation is donoted; $P < 0.05$. The integer to the right of each graph is an index of seasonality discussed in the text and equals the difference between October 1981 and October 1982 divided by maximum variation over the year (%). Sampling time 1 = September–October 1981, 2 = January 1982, 3 = April 1982, 4 = July 1982, 5 = September 1982. a = Missing data.

Prevalence of salmonella by host and season

Of the 19 species of mammals sampled, salmonellae were isolated from 13 species. The pattern of temporal variation in prevalence can be examined only for species from which >50 samples were taken—the northern quoll *Dasyurus hallucatus*, the brindled bandicoot *Isoodon macrourus*, a mosaic-tailed rat *Melomys* sp. cf. *burtoni*, the common rock-rat *Zyzomys argurus* and the large rock-rat *Z. woodwardi*.

Temporal variation in prevalence of all *Salmonella* serotypes is shown in Fig. 1 scaled as a proportion of positive swabs. The data are expressed in three ways: as serotypes per sample, isolates per sample and, in the third column, using the Berger–Parker Dominance Index (*d*). The number of serotypes and number of isolations at different times was examined using 5×2 χ^2 tables. *Z. woodwardi* showed no significant variation over time and is not considered further.

Three species (*Z. argurus*, *D. hallucatus* and *I. macrourus*) showed significant temporal variation in the number of serotypes isolated. Four species (the former plus *Melomys* sp. cf. *burtoni*) showed significant variation over time in the number of salmonella isolations. Three species show similar temporal patterns in both the serotype and isolation numbers with a peak prevalence during the wet season (January sample) and declining or remaining at a low level through the dry season (April, July and September samples). During the wet season the prevalence in *D. hallucatus* also increased but continued to rise after the wet season (April) before declining through the remainder of the dry season. *D. hallucatus* are very mobile and an individual was recorded moving a minimum of 1.5 km in 2 days, between the grids WM and WV.

The temporal changes in serotype diversity show no common pattern between species. *Z. argurus* and

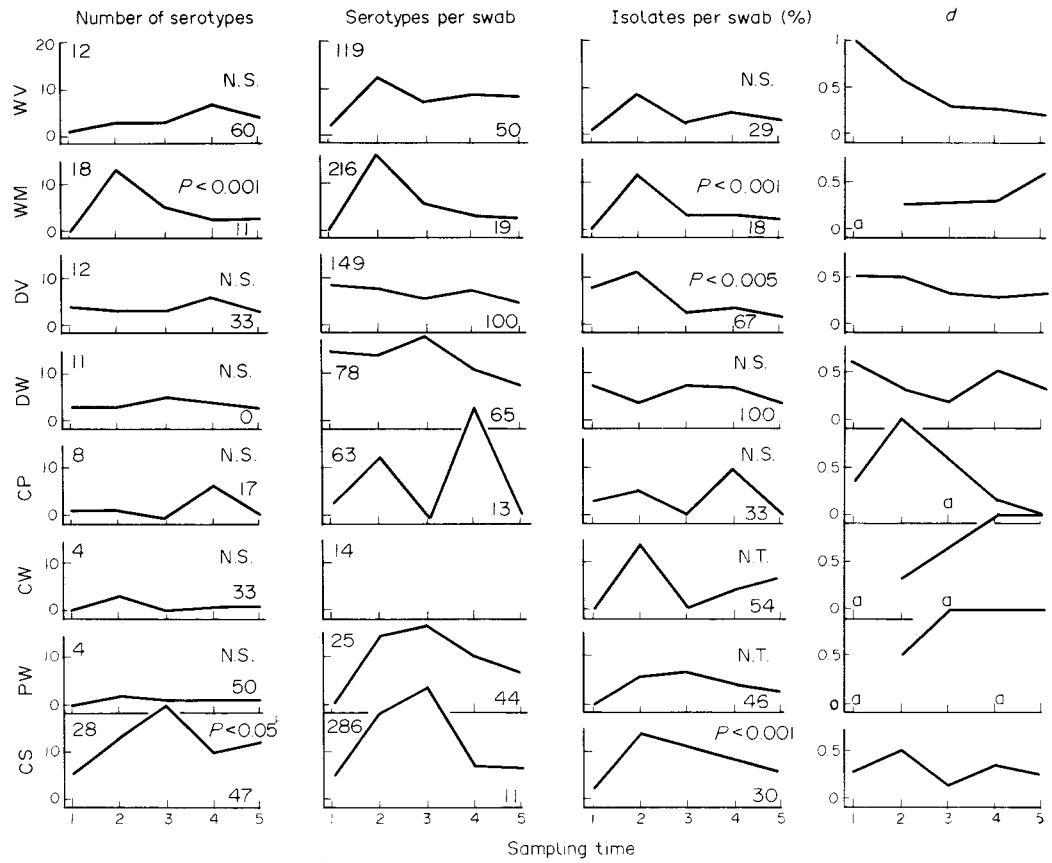

Fig. 2. Seasonal variation in the occurrence of *Salmonella* in the eight capture–mark–recapture sites in the Mitchell Plateau region. The figure is discussed in the text. First column = number of serotypes; second column = serotypes per sample (%); third column = prevalence per sample (%); fourth column = diversity using the Berger–Parker Dominance Index (Fig. 1). The integer to the upper left of each graph is: column 1 = number of serotypes; column 2 = number of samples taken. Other symbols are as described for Fig. 1.

Melomys sp. had a peak in the wet season, but while the latter declined to the end of the dry season (September) *Z. argurus* declined but then increased in September. Diversity of *Salmonella* increased after the wet season (April) and remained high throughout the dry season, while in *I. macrourus* diversity increased steadily with only a slight decline in September.

Although four species show pronounced temporal variability in the prevalence of salmonellae the pattern in *D. hallucatus* differs from that in the other three species. The more pronounced variability in the proportion of isolates compared with the proportion of serotypes results from the logarithmic relationship between the number of samples and the number of serotypes isolated. The lack of overall pattern in diversity, which is not testable statistically, may well reflect the random nature of serotype occurrence by both host and site, as discussed later.

It appears that the temporal pattern is a seasonal pattern. The numbers to the right of each graph in Fig. 1 show the absolute percentage difference between October 1981 and October 1982 divided by the total range in all sampling periods; it is a measure of the difference between samples taken at the same season expressed as a percentage of the annual variation. This index value is generally small (2–18%) for the number of serotypes and isolates but is high in *Melomys* sp. for the number of isolates. This reflects the lack of salmonella in DV in September 1982 compared with the high prevalence seen in September 1981. For diversity, the index is high, consistent with the apparent random variability in serotype occurrence as discussed later.

Temporal changes in prevalence and serotype number in different sites

Figure 2 portrays, for the five sampling times, the number of serotypes, the number of serotypes per sample, the prevalence of salmonella and their diversity for the eight major trapping sites. The number of serotypes isolated from each site shows no consistent pattern over time. The two areas (CS and WM) with sufficient isolates show significant changes in the number of serotypes over time which reflect the pattern of the host species contributing to the data. CS is dominated by isolates from *D. hallucatus* and WM by those from *Melomys* sp. (cf. Fig. 1). The scaled data, expressed as serotypes per unit sample show more consistency with a general increase in the number of serotypes isolated during, and sometimes immediately following, the wet season (January and April).

The third column in Fig. 2 shows the number of salmonellae isolated per sample for each site during the five sampling periods. Two sites (CW and PW) have insufficient data to test for temporal changes. Of the remainder only WM, DV and CS show significant temporal changes in prevalence. Each site shows maximum prevalence during the wet season (January) followed by a decline throughout the dry season (April–October).

Association of serotypes by site, host and mammal communities

Sorensen's index of similarity (α) was determined for the association of serotypes by site, of serotypes in hosts and of the mammal communities by region. The α values were arranged using the furthest neighbour method of GENSTAT into similarity dendrograms to facilitate comparisons (Fig. 3).

Host species grouped according to Salmonella *serotypes.* Three main groups of mammals show $<25\%$ similarity according to their *Salmonella* serotypes. These are (1) *Sminthopsis virginiae* (marsupial) and *Leggadina lakedownensis* (eutherian); (2) *Zyzomys argurus*, *Z. woodwardi*, *Melomys* sp. (eutherians), *Isoodon macrourus, Dasyurus hallucatus* and *Wyulda squamicaudata* (marsupials); (3) *Pseudomys* sp., *P. nanus* and *Rattus tunneyi* (eutherians). Eutherians and marsupials do not group according to the *Salmonella* serotypes they carry, neither do congeneric species living in close proximity; the two *Zyzomys* species are well separated while the two *Pseudomys* species, despite being congeneric show only low similarity.

Figure 3b shows only those species for which $\geqslant 50$ samples were taken. *Z. argurus* and *D. hallucatus* are sympatric, mostly from grid CS, while *Melomys* sp. and *I. macrourus* overlap in their distribution at DV.

Sites grouped according to Salmonella *serotypes.* Three subgroups of sites show $<25\%$ similarity according to the serotypes isolated there (Fig. 3c). These are (1) WV, DW, DV, WM and CS; (2) CP and CW, and (3) PW, RWM and NPW. DW is more similar to the vine thicket at WV than to the contiguous vine thicket DV. The coastal site (WM) is most similar to the most distant and inland site (CS). CP and CW, which are separated by only 1.5 km, group together, as do the two plateau sites (PW and NPW) which are separated by 25 km. Hence there is no clear separation by serotypes of either vegetation associations or regions.

Figure 3d shows the groupings above, considering only sites from which $\geqslant 50$ samples were taken. This emphasises the difference in serotypes between sites and the lack of relationship between vegetation and the 'community' of salmonellae.

Sites grouped according to mammalian species. Four mammal communities are separated by $\leqslant 50\%$

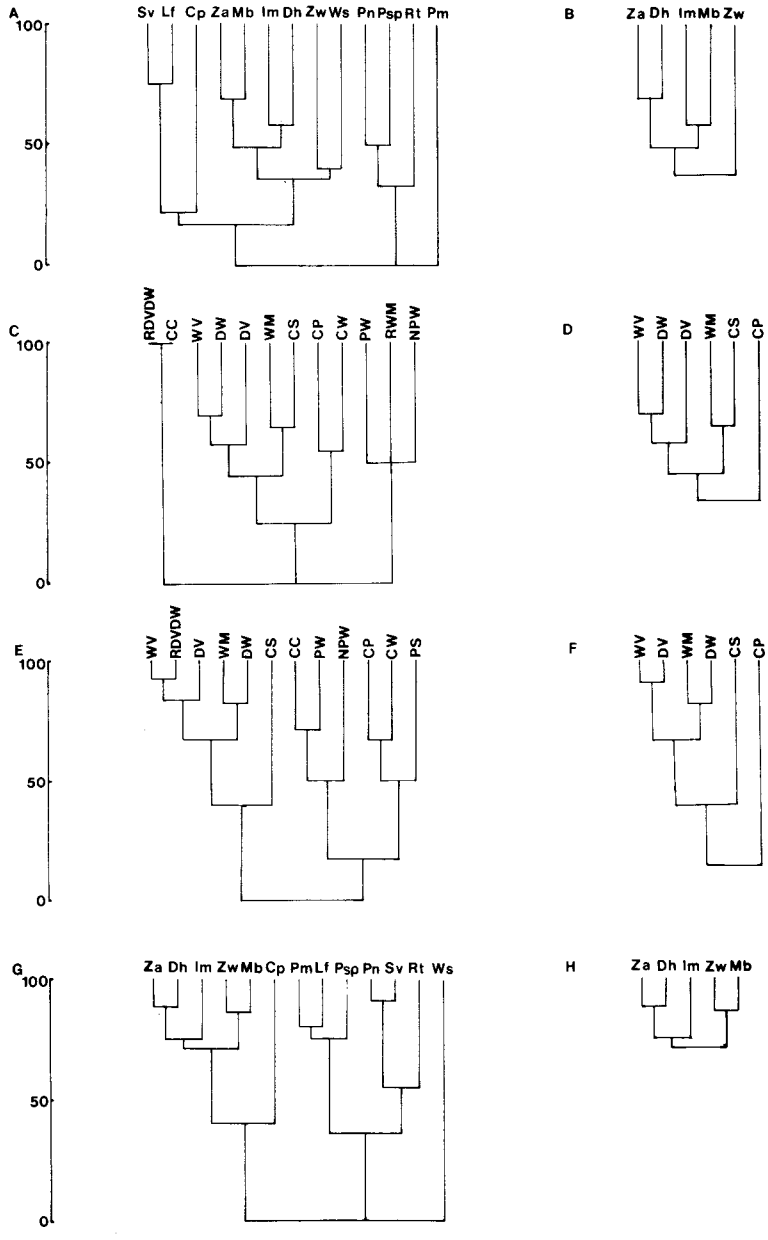

Fig. 3. Dendrograms showing the similarity of the *Salmonella* 'community' in different areas and hosts, the mammal community in different sites and of mammal species according to sites. Details are discussed in the text. (a) Mammal species grouped according to the *Salmonella* serotypes they host. (b) As in (a) but considering only species from which >50 samples were obtained. (c) Sites grouped according to the *Salmonella* serotypes found there. (d) As (c) but considering only sites from which >50 samples were obtained. (e) Sites grouped according to the mammal species trapped. (f) As (e) but considering only sites >50 samples. (g) Mammal species grouped according to the sites on which they occur. (h) As (g) but considering only species from which >50 samples were taken.

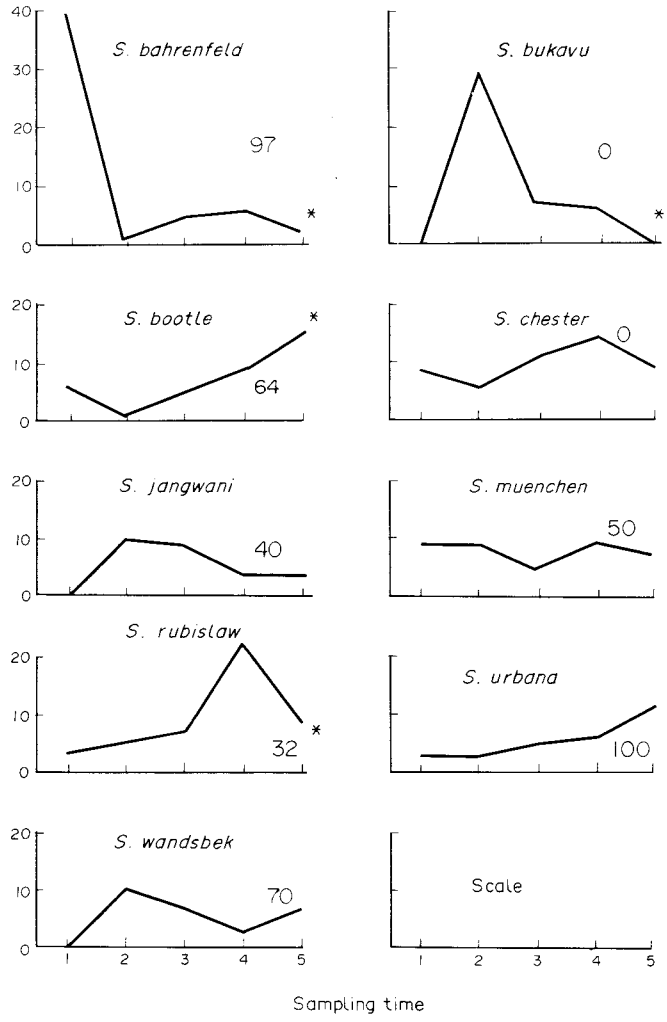

Fig. 4. Seasonal occurrence of isolations of given *Salmonella* serotypes. Integer to the right of each graph is the index of seasonality (see text; * denotes significant temporal variation (Table 8).

similarity (Fig. 3e). The vine thickets (WV, DV and RDVDW) are similar in their mammal communities while the coastal mosaic site (WM) is most similar to the woodland site (DW) adjacent to the vine thicket at DV. The sandstone site (CS) separates clearly from the remainder. The major group CC to PS represent riparian, alluvial and laterite sites of woodland over grass.

Figure 3f shows the same data considering only those sites from which $\geqslant$50 samples were taken. It emphasises the similarity of the mammal communities in the vine thickets and the distinct separation of the alluvial (CP) and the sandstone (CS) sites.

Mammalian species grouped according to sites. Only those mammalian species from which salmonellae were isolated are considered. Two major groups are seen in Fig. 3g. The group *Z. argurus* to *C. pencillatus* represents the group WV to DW in Fig. 3e while the group *P. maculata to R. tunneyi* represents the group CC to PS in Fig. 3e. Figure 3f represents the species for which $\geqslant$50 samples were taken for salmonella isolation as in Fig. 3b. All these species occur jointly on a similar range of sites.

This analysis suggests from the lack of concordance between the dendrograms and the details within them, that (1) vegetation *per se* has no influence on the

salmonellae in an area, (2) the variety of serotypes is not influenced by whether the site is coastal (WV and WM) or inland (CS is the most inland site but is most similar in *Salmonella* serotypes to WM), (3) there is no division of *Salmonella* serotypes according to systematic divisions of the host—marsupials and eutherians do not group according to the *Salmonella* serotypes they carry. Although the two *Pseudomys* spp. do group, they show only 50% overlap which is similar to that between the two *Zyzomys* spp. which show less overlap than 69% of the host species considered, (4) the mammal community within areas (Figs 3e and f) group differently from the community of salmonellae within areas (Figs 3c and d), (5) the groupings of sites using *Salmonella* serotypes (Figs 3c and d) and mammal hosts (Figs 3e and f) are different showing that the groupings of serotypes is unrelated to the mammal community *per se*, (6) the groupings of mammal hosts according to the salmonellae they carry (Figs 3a and b) and by sites (Figs 3g and h) exhibit no concordance, so hosts occurring at the same site do not have a similar range of *Salmonella* serotypes. Note that *I. macrourus* and *Melomys* sp. are closest in Fig. 3b but most distant in Fig. 3h.

Distribution of Salmonella *serotypes by site*

Some *Salmonella* serotypes seem to group by area and time indicating an outbreak focus spreading through the area. Where sufficient data are available serotypes were tested for non-random occurrence by the criteria described in the footnote to Table 4. Given serotypes were significantly concentrated on individual sites in 5 of the 12 combinations tested (Table 4) indicating that the serotype may spread through the population or community once that serotype is present.

Examination of the hosts from which the serotypes were isolated (Table 4) shows that the entire trophic spectrum of the mammals (granivore, herbivore, insectivore and carnivore) may host a given serotype simultaneously at the same locality. In two cases (*S. bahrenfeld* at DV and DW in 9/81 and *S. wandsbek* at DV in 1/82) the top carnivore was infected by another serotype and in neither case was the carnivore infected by the given serotype in the subsequent sampling period.

Host and area specificity of Salmonella *serotypes*

Considering only serotypes for which ≥ 7 isolations were made in 12 sites, there is no evidence of host or area specificity in any serotypes. For each of the 13 serotypes considered, the number of sites on which they were present ranged from 2 to 8 ($\bar{x} = 5.5$, $s = 1.98$). Two serotypes (*bronx* and *oranienberg*) occurred at only two sites (WM and CS). The 13 serotypes considered were present in 13 mammal species with individual serotypes occurring in from 3 to 8 host species ($\bar{x} = 6.1$, $s = 1.32$).

There is no evidence for site or host specificity for any of the *Salmonella* serotypes.

Table 4. Results of tests on the random distribution of isolations of given serotypes in the Mitchell Plateau region. Significant tests indicate concentrations of the serotype in the area

Serotype	Date	Site	G_{adj}	P	Hosts infected in order of herbivores/ insectivores/carnivores
S. bahrenfeld	9/81	DV+DW*	22.67	<0.001	*Melomys* sp., *Z. argurus, Z. woodwardi*/
S. bootle	9/82	CS	3.39	>0.05	
S. bukavu	1/82	DV	1.86	>0.1	
	1/82	WM	4.70	<0.05	*Melomys sp./I. macrourus/D. hallucatus*
	1/82	CS	9.45	<0.005	*Z. argurus*//*D. hallucatus*
S. jangwani	1/82	WM	8.26	<0.005	*Melomys* sp., *Z. argurus, C. penicillatus*/
S. muenchen	1/82	WM	3.13	>0.05	*I. macrourus/D. hallucatus*
	7/82	CS	0.48	>0.1	
S. rubislaw	7/82	CS	2.91	>0.05	
	7/82	WV	0.25	>0.5	
	7/82	DV	0.02	>0.5	
S. wandsbek	1/82	DV	6.93	<0.01	*Melomys* sp.//*I. macrourus*

The data were tested by 2 X 2 tables using the conservative G_{adj} statistic. Cells contained the number of isolations (X) of the given serotype as follows: $X_{1,1}$ = given serotype in given area, $X_{1,2}$ = all other serotypes in given area, $X_{2,1}$ = given serotype in all other areas, and $X_{2,2}$ = all other serotypes in all other areas.

* These sites are combined because they were contiguous trapping grids.

Multiple infections

From October 1981 to October 1982 between 0 and 3 serotypes were isolated per sample ($\bar{x} = 0.297$, $s^2 = 0.240$). The frequency distribution of the number of serotypes per sample follows a Poisson distribution ($\chi^2 = 4.58$ with 3 d.f.; $P > 0.1$) implying that multiple infection occurs at random.

The distribution of joint occurrences ($N = 107$) and the number of isolates ($N = 267$) was used to calculate the expected number of joint occurrences for each serotype. Only *S. bootle* departed from the expected number of joint occurrences with other serotypes [$\chi^2 = 4.03$; $P < 0.05$] and was present in excess. *S. bootle* occurs jointly with 8 other serotypes and was isolated from 7 hosts. This result is of marginal significance and one significant result would be expected by chance as 26 serotypes were involved in joint occurrence with other serotypes.

It is concluded that multiple infections of mammals by *Salmonella* spp. occurs at random; that infection by salmonellae does not predispose the host to concurrent infection by other *Salmonella* serotypes and that the serotypes present do not interact in a positive or negative manner.

It is clear from this analysis that the variablility in prevalence of salmonellae between areas, hosts and season must be explained in a manner independent of the concept of communities of salmonellae in the host. These include (a) presence of *Salmonella* serotypes in the area; (b) seasonal factors influencing the *Salmonella* serotypes themselves; (c) contact between host and salmonellae, e.g. change in location and diet, and social behaviour of host; (d) changes in the susceptibility of the host to infection with salmonellae once they have been ingested; (e) the possibility that the hosts are always infected but the salmonella population is too low for isolation. These will be considered in the general discussion.

Salmonella in specific hosts

In this section attention is directed to changes in the prevalence of salmonella between areas and season in individual host species. Consideration is given only to the species for which sufficient data are available for statistical analysis. The adjusted value of the *G*-statistic, which is distributed as χ^2 with 1 d.f., is used throughout.

Melomys sp. cf. burtoni. The pooled annual data show that *Melomys* has fewer serotypes in WV than in DV ($G = 4.22$; $P < 0.05$) or WM ($G = 5.28$; $P < 0.025$) but that WM and DV do not differ ($P > 0.5$). The prevalence of salmonella follows the same pattern (respectively $P < 0.25$; $P < 0.005$ and $0.1 > P > 0.5$). The coastal sites showed lower annual prevalence ($G = 7.31$; $P < 0.01$) than the inland site (DV).

Analysis of the number of serotypes per sampling period shows no difference between WV, WM, or DV. On the same basis the prevalence of salmonella does not differ for all but one trip when either the three sites (WV, WM and DV) or coastal (WV and WM) and inland (DV) sites, are compared. The exception is October 1981 when no salmonellae were isolated from *Melomys* on coastal sites. Hence DV showed higher prevalence of salmonella than WV ($G = 6.48$; $P < 0.025$) or WM ($G = 10.52$; $P < 0.005$), or both coastal sites combined ($G = 13.80$; $P < 0.005$).

Dasyurus hallucatus. On the pooled annual samples *D. hallucatus* showed a lower prevalence of salmonella at NPW than on all other sites combined ($G = 7.87$; $P < 0.01$). No other sites differed from each other. There was no difference between coastal and inland sites in the prevalence of salmonella in *D. hallucatus,* unlike *Melomys.*

Small sample size prevented detailed analysis of the prevalence of salmonella in *D. hallucatus* during different sampling periods. Generally no statistical differences in prevalence occurred except in April 1982 when NPW showed lower prevalence of salmonella than DV ($G = 5.80$; $P < 0.025$) and CS ($G = 13.25$; $P < 0.005$).

Isoodon macrourus. This bandicoot is distributed widely in the region and sample sizes for individual sites are small. On pooled site data it has been seen that the prevalence is higher in January. Comparison between coastal sites and inland sites shows that the prevalence of salmonella is greater on the coast in January ($G = 4.61$; $P < 0.05$), April ($G = 5.03$; $P < 0.025$), July ($G = 6.50$; $P < 0.025$) and for the pooled annual sample ($G = 8.46$; $P < 0.005$). This is the reverse of the pattern seen in *Melomys.*

Zyzomys argurus. The prevalence of salmonella in the common rock-rat was greater in January than all other trips combined ($G = 53.33$; $P < 0.005$). Sample numbers are too small to treat sites separately except for the sandstone site (CS) so we examined pooled data. The annual period prevalence of infection did not differ between CS and all other sites combined ($G = 0.94$; $P > 0.1$) or between coastal and inland sites ($G = 0.36$; $P > 0.5$). No difference in prevalence was recorded between coastal and inland sites in any season ($P > 0.1$ to $P > 0.9$) or between any two sites on an annual basis ($P > 0.9$).

Gain and loss of salmonella infection in individuals

The sequence of serotypes in individuals sampled during successive seasons provides information on the natural history of salmonella and whether the repeated capture of individuals resulted in the spread of infection. Data are present (Appendix 3) showing the results for individuals from which isolations were attempted in more than one sampling period. From these data true incidence can be determined [9].

Only 50% ($N = 26$) of individuals showed the same serotype on more than one occasion, most frequently (85%) found on the next sampling trip and never separated by more than two ($\bar{x} = 1.15$) sampling periods. This is clearly not random and, as the sequences occur throughout the year, it does not result from the high prevalence found in summer. This result has important implications for the data base and will be discussed later.

Some individuals were sampled repeatedly and no salmonella isolations made, while isolations were made from others each time they were sampled. Other individuals were found with salmonellae and then repeatedly no isolations were made from samples. Others were found with salmonella after repeated negative samples. These data strongly imply a real gain and loss of salmonellae from the individuals rather than false negatives (see General Discussion).

The other factor of relevance to the sampling procedure is the possibility of spreading salmonella infection between sites either on personnel or on apparatus. If this were the case, it would be expected that more individuals would show the sequence of negative–positive than positive–negative (values respectively 26 and 31; Appendix 3) but values for these sequences do not differ ($\chi^2 = 0.44$, $P > 0.5$) indicating no effect of sampling.

GENERAL DISCUSSION

Detection efficiency

It is not possible to test an assumption made in this study that the probability of isolating salmonellae from a sample was not influenced by season or host species. Two factors are pertinent: the chance of detecting salmonellae using the standard isolation method on rectal swabs compared with faecal samples, and the change in efficiency with differing salmonella burdens. In a detailed analysis of these problems on the quokka, Hart *et al.* [10] demonstrated that rectal swabs followed by single enrichment were 67% efficient in isolating *Salmonella* and *Arizona*. Efficiency was increased to 80% by using three swabs divided between two enrichment media. Rectal swabs approached 100% efficiency for salmonella burdens of $>10^3 g^{-1}$ faeces, declining to $\simeq 50\%$ for 10^2–$10^3 g^{-1}$ faeces and 25% for $<10^2$ salmonellae g^{-1} faeces. Faecal samples were found superior in detection of multiple infections.

As Hart *et al.* [10] point out swabs are the preferred method for field studies and they suggest the 3-swab, 2-enrichment procedure for field work where the traditional sampling method of killing and dissecting out organs of interest cannot be justified or negates the purpose of the field programme. Both the latter points apply to this study in which the populations of sometimes little-known animals were being studied through time. However, the recommendations of Hart *et al.* [10] still fail adequately to cover the problem of differential detection rates with different salmonella burdens. This could be overcome only by weighting the incidence levels following the counting of salmonella burdens. Clearly this procedure is uneconomical for general screening of wild populations.

In light of the above, the data on isolation sequences (see previously and Appendix 3) are pertinent. If false negatives were common, one would expect a wide temporal spread in the repeated detection of the same serotype in an individual, but these are separated by $\simeq 1$ sampling interval. This suggests that individuals are acquiring the salmonella infection and losing it, at the outside, within one sampling interval (max. $\simeq 3$ months). This is consistent with findings from domestic animals [11].

Contamination

Salmonella screening was a minor part of a wider study and the field conditions made it impossible to sterilize trapping and handling equipment. Contamination via equipment can occur (S. D. Bradshaw, personal communication) and its role in this study must be examined.

Major cross-contamination in this study would have a number of consequences as the study progressed because the same sites were being examined through time:

(1) The number of serotypes should increase through time on any one site. This cannot be examined simply as additional sampling naturally exposes more serotypes (see footnote to Table 3). However the number of serotypes isolated on each site at the start and end of the programme was generally similar (Fig. 2).

(2) The serotypes isolated from each site should reflect the trapping sequence of sites within grids and the cumulative effect of contamination during the entire programme. This point can be considered by

Table 5. Prevalence of *Salmonella* isolations in non-human vertebrates in various regions

Taxa	Region	Mean incidence and range between species (%)	Number of samples	Number of host species	Number of serotypes	Source
Rodents*	Panama and Columbia	3 (0–7)	318	6	8	[12]
Marsupials*		7 (0–13)	109	4		
Lizards†	Panama	28 (0–50)	548	22	11	[13]
Amphibians†	Panama	4 (0–17)	321	20		
Lizards‡	Panama	29 (6–92)	447	34	26	[14]
Lizards	Texas	49 (0–100)	67	7	2	[15]
Primates§	Panama	2 (0–31)	671	6	8	[16]
Mammals	S. England	1 (0–2)	1269	16	2	[17]
Reptiles	Australia	67‖	116	32	33	[18]
Mammals (1963)	Virginia¶	13 (7–22)	101	5	7	[19]
Mammals (1965–1966)	Virginia ¶	0 (0–4)	217	7	2	[19]
Frogs	India	14‖	129	?	9	[20]
Mammals‡	Panama	3 (0–20)	974	19**	14	[21]
Marsupials	N. Carolina	70‖	≃200	1	6	[22]

* Only one serotype is common.
† Regularly isolated only from hosts occurring near human habitation, bathing areas and pastures.
‡ Prevalence highest in the dry season (January–April).
§ Newly arrived in laboratory.
‖ Prevalence (%) in total study.
¶ Significantly lower prevalence in second survey; note that season of capture varied.
** Including four *Arizona* and *Edwardsiella.* Isolated mostly from near areas of human habitation.

reference to grid CS which had the greatest diversity of serotypes (Table 1) and most *D. hallucatus* which itself harboured most serotypes (Table 2) and was sympatric with the main population of *Zyzomys argurus*. The serotype diversity and prevalence of salmonella was maximal in *D. hallucatus* in April 1982, at which time they had declined in *Z. argurus* and other species (Figs 1 and 2). The data do not suggest major cross-contamination of other species or sites from *D. hallucatus* The most telling data came from the September 1981 trip when no salmonella were isolated from either of the coastal sites (WV and WM) despite several grids having previously been trapped including grid CS. Such failure to detect salmonella on specific grids is seen throughout the programme.

(3) The salmonella 'communities' should become progressively more similar as the programme progressed. If this were true the frequency of the most common serotypes should decline through time whereas there is no trend in the data. The nine most common serotypes comprise 71, 76, 65, 83 and 65% of all serotypes isolated in successive trips.

None of the control swabs taken from handlers and handling equipment detected any salmonella despite one *Arizona* being detected.

Although minor contamination cannot be excluded, there is no evidence from any of our data that any serious cross-contamination has occurred.

Prevalence compared with other studies

Direct comparison of prevalence levels with other studies is compounded by differing techniques and lack of information to make some subdivisions. Most studies of salmonella prevalence use bulk samples from alimentary tract or tissue of killed animals and are thus more likely to detect salmonella and detect multiple infections (see previous discussion).

Table 5 shows prevalences of salmonella for studies from other taxa and regions. Maximum prevalences of salmonella in mammals are markedly higher in the Mitchell Plateau area than in most other regions.

The finding of a greater prevalence of salmonella in marsupials compared with that in eutherians in the Mitchell Plateau area (Table 3) has also been reported for Central America [21].

Causes of seasonality in the prevalence of Salmonella

Salmonellae, whether wet or dry, are rapidly killed by exposure to solar radiation but survive well in its absence [23]. Given the thermal equitability of the climate of the northern Kimberley region the most pertinent climatic effects are likely to be the seasonality in rainfall and solar radiation. Due to high summer cloud cover, the solar radiation varies little over the year ($\simeq$ 1.3 times) compared with an area such as Perth ($\simeq$ 2.8 times) which has pronounced summer maximum radiation and winter rainfall. In the Perth area highest prevalence of salmonella occurs in quokkas in the summer [24].

In the few detailed studies of salmonella prevalence in wild animals, marked seasonality has been observed occurring in all seasons in different climates (Table 6). So the greatest prevalence may occur in summer or winter when the weather is dry or wet and hot or cold. The seasonality in prevalance is thus probably not associated with the effects of weather on salmonellae but should be sought in the predisposition of animals to infection by salmonellae.

Experimentally, numerous factors have been shown to influence the susceptibility of animals to infections by salmonella. Mostly they may be grouped under the general term 'stress factors', where true changes in susceptibility occur, and behavioural factors where the probability of being exposed to salmonellae is changed (Table 7). The 'stress factors' may reduce the

Table 6. The relationship between weather, season and the maximum prevalence of *Salmonella*

Taxon	Season of maximum prevalence	Relative weather conditions at max. prevalence	Source
Reptiles	Winter (January–April)	Cold, dry	[14]
Setonix brachyurus	Summer	Hot, dry	[24]
Flies	Summer	–	[25]
Dasyurus hallucatus	Autumn	Hot, dry	This study
Isoodon macrourus	Summer	Hot, wet	This study
Melomys sp.	Summer	Hot, wet	This study
Zyzomys argurus	Summer	Hot, wet	This study

Table 7. Factors increasing the susceptibility or chance of exposure to salmonella infection

Taxon	Conditions	Source
Stress factors		
Humans	Diseases	[26]
Mice	Food and water deprivation	[27]
Cattle	Food deprivation	[28]
Sheep	Food deprivation	[11]
Cattle	Disease and environmental discomfort	[29]
Pigs	Stress	[30]
Quokka *Setonix brachyurus*	Starvation in the wild	[24]
Behavioural factors		
Rats	Feeding habits	[31]
Birds and small mammals	Sociality?	[32]

infective dose of salmonella [11] or within 2–3 days [27] permit an increased burden in already infected animals. Salmonellae can be eliminated from the alimentary tract following a stress-induced increase [11]. The stress involved may be quantitative (Table 7) or qualitative, such as sudden changes in diet [27].

At this stage it is not possible to comment on potential causes of seasonality in the prevalence of salmonellae in the Mitchell Plateau area. The coincidence of the marked rise in prevalance with the wet season differs in pattern from some other studies (Table 7). The wet season marks the end of a 7-month drought. Grasses and the deciduous elements in the vine thickets respond quickly and free water becomes generally available. Intuitively the dry season would appear to be a period of stress which, according to experimental evidence, should increase the susceptibility of animals to salmonella infection (Table 7). This is the reverse of the trends in the Mitchell Plateau area. The numbers of individuals of *Z. argurus, Z. woodwardi, D. hallucatus* and *Antechinus bilarni* declined during the wet season in the Northern Territory [33–35]. Begg [35] considered the wet season stressful for both *Zyzomys* species due to lack of seed during that season but demonstrated that lowest body weight occurred towards the end of the dry season. He considered the dry season most stressful for *D. hallucatus* due to food shortage [34].

The present data indicate, by analogy with experimental studies on salmonellae, that for at least four species of mammals the wet season in the Mitchell Plateau area is stressful. Screening for salmonella may be a useful tool for assessing the physiological status of terrestrial vertebrates in the wild.

Further comment on 'stress' factors will be made when analysis on the breeding and physiological status of the mammals is completed. Of particular relevance will be the measurement of free corticosteroid levels in the populations examined for salmonellae since these are indicative of stress in mammals. They will be considered in conjunction with plasma nutrients, water turnover and haematological measures to elucidate the host condition in relation to the prevalence of salmonella.

Effect of Salmonella *on the animals*

Animals are frequently symptomless carriers of salmonellae but in acute infections rodents and foxes suffer high (80%) mortality, the rodents dying within a day of the onset of clinical symptoms. Symptoms include inappetence, diarrhoea and rapid loss of weight; those surviving are listless for several days with intermittent diarrhoea [23]. Together these factors would result in low survival of wild animals with acute infection and a low probability of catching, in a study of this type, small mammals with acute salmonellosis. It is unlikely that the quantitative effects of salmonellae on wild populations can be described.

Implications for salmonella surveys

Concurrent marked seasonality in the prevalence of salmonella infection in several species of wild animals in a number of distinct habitats has never previously been reported. Indeed, detailed analysis of seasonal changes in prevalence have only been seen in the quokka in a managed ecosystem with considerable human contact [24] .These findings of marked seasonality in prevalence are important for the design

of surveys for salmonellae and, by implication, probably for all zoonoses.

A one-off survey of the two coastal sites (WV, WM) in October 1981 would have failed to record a single salmonella infection while comparison of coastal and inland sites at the same time would have led to the conclusion that there was a lower prevalence on coastal than inland sites. As has been shown, on an annual basis, there are either no differences, or real differences in prevalence (with coastal sites higher or lower than inland sites), depending on which host species is considered. With a single survey, conclusions on the prevalence of salmonella within the same habitat could depend on the site considered; for example, the vine thickets at DV and WV differed markedly in October 1981 but were otherwise similar.

It is apparent that broad-scale surveys for salmonellae should include a range of habitats, which should be replicated and repeated over several seasons. Certainly, if objective conclusions are to be reached large numbers of swabs are required; this is apparent in the present work where there is sufficient information for only four species from which to analyse, more than superficially, the spatial and temporal components of salmonella distribution.

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APPENDIX 1

Salmonella serotypes isolated from the Mitchell Plateau region between October 1981 and October 1982. χ^2 tests for seasonal variation in a given serotype compared with seasonal distribution of all serotypes. Serotypes with <19 isolations were not tested

Serotype	Proportion of all isolations (%)						Test of temporal variation		
	Per trip					Total			
	9/81	1/82	4/82	7/82	9/82		χ^2	d.f.	*P*
adelaide		–	1			0.3	–		
angoda			1			0.3	–		
bahrenfeld	39	1	5	6	2	7.5	51.37	3	<0.005
ball			1	1	2	0.9	–		
bleadon			1	1		0.6	–		
bootle	6	1	5	9	15	6.9	9.87	3	<0.025
bournemouth			1			0.3	–		
brisbane	6	1	1			1.2	–		
bronx		2	3		7	2.1	–		
bukavu		29	7	6		10.7	37.30	4	<0.005
charity		1	1	1		0.9	–		
chester	9	6	11	14	9	9.9	2.83	3	>0.1
eastbourne	6	3		3	2	2.7	–		
fremantle	12					1.2	–		
give		1				0.3	–		
havana		1				0.3	–		
houten				4		1.2	–		
hvittingfoss	3	2	1		2	1.5	–		
jangwani		10	9	4	4	6.6	3.17	2	>0.1
kalumburu				1			–		
kimondoni		2				0.6	–		
kisarawi					2	0.3	–		
litchfield			3			0.6	–		
lohbruegge		1				0.3	–		
muenchen	9	9	5	9	7	8.1	0.49	2	>0.1
ohlstedt		3	5	1	7	3.3	–		
oranienburg		2	4	4	7	3.6	1.96	2	>0.1
ord					2	0.3	–		
orion			1			0.3	–		
poona			7			1.5	–		
potsdam			1	1		0.6	–		
rubislaw	3	5	7	22	9	10.4	17.30	3	<0.005
singapore				2		0.3	–		
thompson					2	0.3	–		
treforest			1		2	0.6	–		
uphill		1	1			0.6	–		
urbana	3	3	5	6	11	5.7	3.38	3	>0.1
wandsworth	3	1				0.6			
wandsbek		10	7	3	7	6.0	3.95	2	>0.1
S.4.5. b:-					2	0.3	–		
Total isolates	33	86	74	96	46	335			

S. arizonae and *S. zehlendorf* were isolated in November-December 1982. One *Arizona* sp. was isolated from a control swab taken from the hand of a field worker. This was the only positive control swab. One *Arizona* was isolated from *I. macrourus* (NPW 12/82). *Edwardsiella tarda* was twice isolated from female *D. hallucatus* (CS 5/82 and WV 8/82).

APPENDIX 2

Salmonella and *Arizona* samples isolated from reptiles in the Mitchell Plateau region. Those marked* were taken in November 1982

Family and species	Number of samples	*Salmonella* serotypes isolated	Isolations per swab (%)
Gekkonidae			
Diplodactylus stenodactylus Boulenger	1	–	
Gehyra australis Gray	1	–	
Heteronotia spelea (Kluge)	1	–	
Nephrurus asper Günther	1	*bahrenfeld*	
Rhynchoedura ornata Günther			20
Agamidae			
Diporiphora albilabris Storr	2	*ball*	
D. bennettii (Gray)	1	–	
D. superba Storr	1	–	
Gemmatophora gilberti (Gray)	1	*bootle*	40
Scincidae			
Carlia foliorum (De Vis)	1	–	
C. johnstonei Storr	1	–	
Ctenotus inornatus (Gray)	9	*bootle,* poona**	
C. robustus Storr	6	*chester*	
Omolepida maxima Storr	1	–	
Sphenomorphus isolepis (Boulenger)	3	–	
Tiliqua scincoides (Shaw)	2	*bootle,* urbana,* Arizona* (not typed)*	26
Varanidae			
Varanus acanthurus Boulenger	4	*bahrenfeld, jangwani, poona*	
V. glauerti Mertens	1	*bahrenfeld, Arizona* 26:26:25	
V. mitchelli Mertens	1	*bahrenfeld, potsdam*	
V. scalaris Mertens	4	*chester, oranienburg, poona* (2) *rubislaw, urbana*	(2)
V. tristis (Schlegel)	1	*urbana*	118
Total	44	11	50

APPENDIX 3

Sequences of *Salmonella* isolations in the same individual on 5 sampling periods. –, no sample: 0, sampled but no *Salmonella* isolated

Individual		Sampling period				
		9/81	1/82	4/82	7/82	9/82
D. hallucatus	1	0	–	–	–	0
	2	–	–	*uphill*	–	*eastbourne*
	3	–	–	–	*eastbourne*	*muenchen* *ord*
	4	–	–	–	*urbana*	*ohlstedt*
	5	*rubislaw*	*give*	*bleadon* *bootle*	*chester* *bootle*	*oranienburg*
	6	–	*bukavu*	*bahrenfeld*	–	0
	7	–	*rubislaw*	*chester*	*rubislaw*	–
	8	–	–	*angoda* *ball*	*chester*	*chester*
	9	–	–	*chester* *ohlstedt*	*oranienburg* *rubislaw*	
	10	–	–	*muenchen*	*chester* *muenchen*	–
	11	–	–	*chester*	*houten* *chester*	0
	12	–	–	*wandsbek* *rubislaw*	*muenchen* *rubislaw*	–
	13	–	–	*bootle*	*bootle*	–
	14	–	–	*rubislaw*	*bukavu*	*bukavu*
	15	–	–	*oranienburg*	0	–
	16	–	–	*charity*	*muenchen*	
	17	–	–	*bukavu*	0	*bootle* *oranienburg*
	18	–	–	*wandsbek*	0	*treforest*
	19	–	–	*bukavu* *jangwani*	*rubislaw*	*muenchen*
	20	–	–	*brisbane*	*wandsbek*	–
	21	–	–	*bukavu*	*rubislaw*	–
	22	–	–	–	*bootle* *rubislaw*	*bootle*
	23	–	–	–	*chester*	0
	24	–	–	–	*bahrenfeld*	0
	25	–	–	–	*oranienburg* *bootle* *muenchen*	0
W. squamicaudata	1	0	–	–	0	0
	2	0	*chester*	–	–	0
	3	0	–	–	0	0
	4	–	*eastbourne*	–	0	–
	5	–	0	*hvittingfoss* *bukavu* *chester*	–	–
	6	–	–	–	*houten* *rubislaw*	0
	7	–	–	–	*rubislaw*	*rubislaw*
	8	–	–	–	0	0

APPENDIX 3. *(continued)*

Individual		Sampling period				
		9/81	1/82	4/82	7/82	9/82
I. macrourus	1	0	*bootle muenchen*	–	–	–
	2	0	*jangwani*	*jangwani*	–	*hvittingfoss*
	3	0	*rubislaw*	–	–	–
	4	0	–	*wandsbek*	–	–
	5	–	–	–	0	*kalumburu*
	6	0	*urbana eastbourne*	0	–	–
	7	0	0	*muenchen*	*muenchen*	*wandsbek*
	8	0	0	–	*urbana*	0
	9	0	–	*ohlstedt*	0	0
	10	*wandsworth*	0	–	–	–
	11	–	0	0	0	0
	12	–	*wandsbek*	0	–	–
	13	–	*bukavu*	0	0	0
	14	–	0	*adelaide*	–	0
	15	–	–	0	*muenchen*	0
	16–18	–	–	0	0	–
	19	–	–	*jangwani*	*bahrenfeld*	0
	20	–	–	–	*bahrenfeld*	0
	21				*rubislaw*	0
	22–25	–	–	–	0	0
	26	–	–	–	0	*muenchen*
	27	–	–	–	*urbana*	0
	28	–	–	–	*singapore*	0
Melomys sp.	1	0	*ohlstedt kinondoni*	0	0	0
	2	0	*muenchen*	0	*muenchen*	0
	3	0	*bukavu*	0	0	–
	4,5	0	–	0	0	0
	6	0	0	0	0	0
	7	0	*jangwani bukavu*	0	0	0
	8	0	0	–	–	–
	9	0	–	–	0	–
	10	0	*bronx*	–	–	–
	11	–	0	–	0	–
	12	–	0	*poona*	0	0
	13–20	–	–	0	0	0
	21–30	–	–	0	0	–
	31	–	–	*poona*	0	–
	32	–	–	0	0	*urbana*
	33	–	–	0	–	0
	34–46	–	–	–	0	0
	47	–	–	0	0	–
	48	–	–	–	*chester*	0
	49	0	–	–	0	0
	50	0	–	–	0	–
	51	–	0	–	0	–

APPENDIX 3. *(continued)*

Individual		Sampling period				
		9/81	1/82	4/82	7/82	9/82
Z. argurus	1	–	–	–	0	0
	2	–	0	–	–	0
	3–7	–	–	–	0	0
	8–10	0	0	–	–	–
	11	0	*wandsbek*	–	–	–
	12,13	0	*bukavu*	–	–	–
	14	0	–	–	0	–
	15	0	–	0	0	–
	16	–	0	–	0	–
	17	–	*bukavu*	0	–	–
	18,19	–	–	0	0	–
	20	0	*wandsbek*	0	–	–