DISTRIBUTION OF SPECIES OF TRICHOSTRONGYLOID NEMATODE PARASITES IN THE SMALL INTESTINE OF THE BUSH RAT, *RATTUS FUSCIPES*

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Summary

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The distribution of three trichostrongyloid nematodes, *Nippostrongylus magnus* (Mawson, 1961), *Odilia bainae* Beveridge & Durette-Desset, 1992 and *Paraustrostrongylus ratti* Obendorf, 1979, in the small intestine of bush rats, *Rattus fuscipes*, was investigated. Each of these species exhibited a significantly different longitudinal distribution within the small intestine. Interactions between the three species, identified by comparisons of the fundamental and realised overlaps in nematode distributions, were the probable cause of the differences in distribution between species. The different distributions, which are here interpreted as niches, occupied by the nematode species are consistent with the hypotheses that *O. bainae* was probably a parasite of hydromyine rodents which filled a vacant niche when it switched to *R. fuscipes* as a host, while *P. ratti* probably occupied another vacant niche when it switched to *R. fuscipes* from an original marsupial host.

KEY WORDS: Parasite, ecology, niche, Trichostrongyloidea, *Rattus*, interaction.

Introduction

One mode by which parasite evolution may occur is "host switching" (Chabaud 1965). This involves a break-down in host specificity allowing the transfer of a parasite from its usual host to an unrelated host species occupying the same environment. The new host may be infected through the skin by free-living stages of the parasite or may ingest the infective form of the parasite with its food (Chabaud 1965). The mechanism of host switching appears to be common among parasitic nematodes (Chabaud 1982) and is based on the assumption that the invading nematode parasite is occupying a previously vacant niche within the new host. In the case of intestinal parasites this is usually defined as a restricted longitudinal or radial distribution within the gut of the host (Schad 1963). Host switching within the nematode superfamily Trichostrongyloidea is well documented (Durette-Desset 1985), yet few studies have examined whether the invading nematode actually occupies a separate or previously-vacant niche.

The trichostrongyloid nematode parasites of the native bush rat, *Rattus fuscipes*, offer the opportunity to examine such an hypothesis. At one locality in Victoria (Blackwood) Obendorf (1979) found that *R. fuscipes* was parasitised by three species of trichostrongyloids, the heligmosomes *Nippostrongylus magnus* (Mawson, 1961) and *Odilia bainae* Beveridge & Durette-Desset, 1992 and the herpetostrongylid *Paraustrostrongylus ratti* Obendorf, 1979 (Obendorf 1979; Beveridge & Durette-Desset 1992 a,b, 1993). *P.*

ratti belongs to a genus which otherwise occurs exclusively in marsupials and which presumably has switched to its current eutherian host (Obendorf 1979). It is considered (Obendorf 1979) to be one of only two examples of trichostrongyloid nematodes switching from marsupials to native rodents, the other being *Woolleya hydromyos* in the water rat, *Hydromys chrysogaster* (see Mawson 1961, 1973). *O. bainae* belongs to a genus which is parasitic primarily in hydromyine rodents and species of the genus were considered by Durette-Desset (1985) to have switched secondarily to murine rodents such as *R. fuscipes*. Only *Nippostrongylus magnus* can be considered an original parasite of this murine rodent (Beveridge & Durette-Desset 1992a).

The current study was therefore undertaken to determine the ecological niches occupied by *N. magnus*, *O. bainae* and *P. ratti* within the small intestine of *R. fuscipes* and to examine the extent of overlap between them to establish whether or not each occupies a distinctive intestinal niche.

Materials and Methods

Ten bush rats, *Rattus fuscipes*, were trapped from along the banks of the Lerderderg River, Blackwood, Victoria, Australia (37° 29' S, 144° 19' E) using collapsible aluminium traps baited with peanut butter. Immediately following euthanasia with chloroform, the small intestine was removed and divided into sixteen equal parts. The total length of the small intestine was measured. Gut segments were incubated in saline at 37°C for at least 2 hours and all nematodes which emerged from the mucosa were fixed in hot 70% ethanol before being counted. *P. ratti* was distinguished

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from other species based on the description of Obendorf (1979) using a stereomicroscope, whereas *N. magnus* and *O. bainae* were differentiated using the descriptions of Beveridge & Durette-Desset (1992 a,b) and a compound microscope following clearing in lactophenol. The rats were also routinely examined for other helminth parasites.

The number of each species of nematodes in individual sections of the small intestine was converted to a percentage of the total number of each species present. For each species, the positions of the anterior, median and posterior nematodes were determined using the method of Bush & Holmes (1986), such that the section number in which nematodes occurred was converted to a percentage of the total length of the small intestine. It was assumed that nematodes were uniformly distributed within each section.

Differences in distribution between species were tested statistically using values calculated from a 2 x 5 contingency table (species x sector of intestine) for each species pair. Sections 5 to 16 of the intestine, where very few nematodes were found, were combined to form a single cell in the table.

The extent of niche overlap between the three species was determined using the equation

$$Cxy = 1 - \tfrac{1}{2}(\Sigma|Px_i - Py_i|)$$

where

$$Px_i = \frac{x_i}{X} \quad , \quad Py_i = \frac{y_i}{Y}$$

(Hurlbert 1978)

such that Px_i and Py_i are the proportions of two species, x and y, in different segments of the intestine

This equation was used to calculate the "fundamental overlap" between species pairs, which is the extent of overlap (Cxy) in the mean distributions of the two nematode species and the "realised overlap" which is obtained by determining the extent of overlap (Cxy) between two nematode species in individual rats and then computing the average of the individual overlaps.

Differences between fundamental and realised overlaps, that is when the realised overlap was substantially less than the fundamental overlap, were used to infer the presence of competition between nematode species.

Seven laboratory rats, *R. norvegicus*, were infected either subcutaneously or orally with 200 - 900 infective

larvae of *N. magnus* or *O. bainae* (Table 3). The infective larvae were obtained by culturing a mixture of faeces from naturally infected rats with activated charcoal on moist filter paper and recovering developed larvae by sedimentation in water. Larvae were separated on the basis of morphological differences (shape of the tail) identifiable using a stereomicroscope (unpublished observations). Infected rats were killed with chloroform 14 days after infection and the distribution of nematodes in the small intestine determined in a similar fashion to that described above. Experimental infections with *P. ratti* via oral, subcutaneous and percutaneous routes were unsuccessful

Results

Nematode distributions in wild rats

N. magnus occurred in 100% of the wild bush rats examined, with a mean intensity of 67 and a range of 11-183. *O. bainae* was present in 100% of wild rats examined, with a mean intensity of 64 and a range of 11-173. *P. ratti* was present in 90% of wild rats examined with a mean intensity of 171 and a range of 1-1094 (Table 4).

Other parasites found in the ten naturally infected bush rats were very small numbers of *Capillaria* sp. (Nematoda) in the first segment of the small intestine and *Capillaria gastrica* (Baylis, 1926) within the squamous epithelium of the stomach in five rats. There was no pathological reaction to adult *Capillaria* or eggs within the squamous epithelium. *Heterakis spumosa* (Schneider, 1866) was found in the large intestine of eight rats. The cestodes *Choanotaenia ratticola* (Sandars, 1957), *Hymenolepis diminuta* (Rudolphi, 1819) and *Bertiella anapolytica* Baylis, 1934 were found in the small intestine. *C. ratticola* inhabited the opening of the bile duct, causing hyperplasia of the bile duct epithelium. *H. diminuta* and *B. anapolytica* were found in segments 4-12 and 5-16 respectively. However, *H. diminuta* was distributed anteriorly to *B. anapolytica* when both species occurred in rats.

N. magnus occurred mainly (64%) in the anterior two segments of the small intestine in naturally infected rats, with maximum intensity in the first segment, and its numbers declined progressively in the remaining sections (Fig.1). The majority of *O. bainae* (82%) inhabited the five most anterior segments in naturally infected bush rats with a maximum intensity (30%) in the second segment (Fig. 1). The majority of *P. ratti* (87%) were distributed throughout the five anterior segments of the small intestine in naturally infected rats (Fig. 1) with maximum intensity occurring in segments 1 to 4. Small intestine lengths ranged from 56-92 cm (mean 71 cm) and hence the average length of each segment was 4.5 cm.

TABLE 1. *Position of mean anterior, median and posterior individuals (± standard error of mean) of* Nippostrongylus magnus, Odilia bainae *and* Paraustrostrongylus ratti *as percentage distances along the small intestine in ten naturally infected bush rats,* Rattus fuscipes.

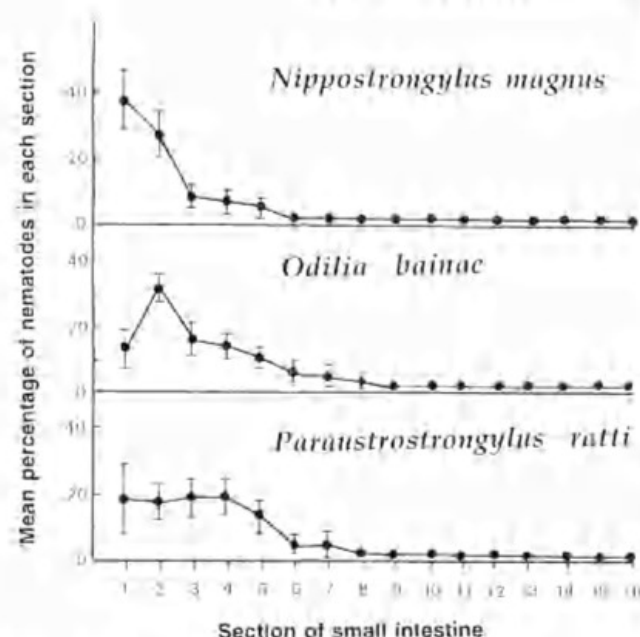|	Anterior	Median	Posterior
N. magnus	1.01 ± 0.64	15.14 ± 4.84	56.63 ± 10.17
O. bainae	2.17 ± 0.84	18.23 ± 3.07	48.40 ± 6.47
P. ratti	3.22 ± 1.62	19.06 ± 2.25	49.40 ± 4.42

Fig. 1. Distribution (mean percentage ± standard error [error bars]) of *Nippostrongylus magnus*, *Odilia bainae* and *Paraustrostrongylus ratti* in each segment (sixteenths) of the small intestine of ten naturally infected bush rats, *Rattus fuscipes*.

N. magnus, *O. bainae* and *P. ratti* were sequentially distributed along the small intestine of naturally infected bush rats but differed in the positions of their mean anterior, posterior and median individuals (Table 1). The mean anterior and median individuals of *N. magnus* were anterior to those of *O. bainae* which were more anterior to those *P. ratti*. However, the mean posterior individual of *N. magnus* was posterior to both *O. bainae* and *P. ratti*. This was due to *N. magnus* inhabiting the posterior quarter of the small intestine in two rats, whereas *O. bainae* and *P. ratti* were not found in this segment. The distributions of the three nematode species were significantly different. Chi-squared values obtained for pair-wise comparisons were *N. magnus* - *O. bainae*, $\chi_i^2 = 77.5$ (p < 0.001), *O. bainae* - *P. ratti*, $\chi_i^2 = 90.9$ (p < 0.001), *N. magnus* - *P. ratti*, $\chi_i^2 = 18.5$ (p < 0.001). There was no correlation between mean positions of nematodes with intensity of infection, except in the case of the posterior position of *O. bainae* ($r^2 = 0.68$, p = 0.004).

The variation in numbers of trichostrongyloid nematodes in each segment of the intestine of naturally infected bush rats was large (Table 4), with the standard deviation equal to or greater than the mean (see standard error bars in Fig. 1). Despite this variation, the difference in distribution was greater in individual rats (1- realised overlap) than the difference in their mean distributions (1- fundamental overlap). The realised overlap was lower than the fundamental overlap in 25 of 28 species interactions. The mean realised overlap between *N. magnus* and *P. ratti* was lower than the overlap between *N. magnus* and *O. bainae* and between *O. bainae* and *P. ratti* (Table 2). The total numbers of each species of nematode in individual rats and the realised overlaps in natural infections varied between individuals but the two parameters were independent of one another ($r^2 < 0.3$). *Capillaria* sp. occurred in such low numbers that

TABLE 2. *Fundamental and realised overlap between niches of* Nippostrongylus magnus, Odilia bainae *and* Paraustrostrongylus ratti *in the small intestine of ten naturally infected bush rats,* Rattus fuscipes.

Nematode species pair	No. of rats infected with both species	Fundamental overlap	Realised overlap (± standard deviation)
N. magnus – *O. bainae*	10	0.68	0.55 ± 0.14
N. magnus – *P. ratti*	9	0.61	0.40 ± 0.27
O. bainae – *P. ratti*	9	0.82	0.55 ± 0.23

TABLE 3. *Percentage of* Nippostrongylus magnus *and* Odilia bainae *occurring in 16 segments of the small intestine of laboratory reared* Rattus norvegicus *following oral or percutaneous infection with third stage larvae*

Segment no. of intestine	Mean percentage of nematodes in segment (± standard error)	
	Nippostrongylus magnus	*Odilia bainae*
No. of rats	4	3
1	85.3 ± 13.1	91.0 ± 5.8
2	2.3 ± 2.2	7.0 ± 6.7
3	2.5 ± 2.5	2.3 ± 2.3
4	10.0 ± 6.8	0
5 – 16	0	0

TABLE 4. *Numbers of nematodes*, Nippostrongylus magnus, Odilia bainae *and* Paraustrostrongylus ratti *in sections (1–16) of the small intestine of ten naturally infected bush rats*, Rattus fuscipes.

Section of intestine	Rat number									
	1	2	3	4	5	6	7	8	9	10
1	14,5,0	0,0,1	2,1,1	5,0,1	31,11,0	5,13,7	42,22,10	42,2,2	37,3,1	49,4,238
2	1,0,0	8,9,8	6,18,0	19,3,5	0,16,0	8,32,6	4,31,36	29,11,1	33,17,19	40,16,366
3	2,0,0	2,6,2	1,9,0	3,3,2	3,36,2	0,9,6	4,9,25	20,10,5	13,7,40	11,2,225
4	2,3,0	1,1,2	3,7,0	8,2,13	0,12,0	1,0,12	4,7,56	7,21,18	3,12,26	9,5,133
5	0,2,0	0,0,0	6,1,0	5,5,18	0,13,1	0,9,0	3,2,16	1,9,9	3,10,34	9,2,76
6	0,1,0	0,0,1	0,0,0	2,4,4	2,4,0	0,6,1	0,1,22	0,1,4	1,17,10	4,3,39
7	0,0,0	0,0,0	0,0,0	10,3,18	0,1,0	0,7,0	0,0,7	0,5,1	0,30,11	2,0,15
8	0,0,0	0,0,0	0,0,0	2,1,4	2,5,0	0,1,2	0,1,5	0,1,1	6,25,2	1,0,2
9	0,0,0	0,0,0	0,0,0	2,1,2	2,2,0	0,0,0	0,0,1	0,0,1	13,13,1	0,0,0
10	0,0,0	0,0,0	0,0,0	1,0,1	1,1,0	0,0,0	0,0,0	0,0,0	12,13,1	0,0,0
11	0,0,0	0,0,0	0,0,0	1,0,1	1,1,0	0,0,0	0,0,0	0,0,0	12,13,1	0,0,0
12	0,0,0	0,0,0	0,0,0	1,0,1	1,1,0	0,0,0	0,0,0	0,0,0	12,13,0	0,0,0
13	1,0,0	0,0,0	0,0,0	10,0,0	0,0,0	0,0,0	0,0,0	0,0,0	10,0,0	0,0,0
14	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0	0,0,0	0,0,0	0,0,0	10,0,0	0,0,0
15	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0
16	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0	0,0,0	0,0,0	0,0,0	9,0,0	0,0,0
Total	20,11,0	11,16,14	18,36,1	96,22,70	43,103,3	14,77,34	57,73,178	99,60,42	183,173,146	125,32,1094

its possible interactions with the trichostrongyloid nematodes were not considered.

Nematode distributions in experimentally infected rats

N. magnus occurred primarily in the anterior segment of experimentally infected laboratory rats, with a relatively small population of nematodes established in segments 2 to 4 (Table 3). Similarly, *O. bainae* became established primarily in the first segment of the intestine, with small numbers of nematodes present in segments 2 to 3. The mean intensity of infection was 10 for *N. magnus* and 14 for *O. bainae*.

Discussion

The significantly distinct sequential distributions of the three species of trichostrongyloid nematode along the small intestine in natural infections and experimental infections suggest that each species occupies a distinct niche. Furthermore, the fundamental overlaps in natural infections between the species pairs *N. magnus* - *O. bainae* (68%) and *N. magnus* - *P. ratti* (61%) were lower than the 70% value suggested by several authors (Pianka *et al.* 1979; Holmes & Price 1980; Bull *et al.* 1989) to indicate the existence of ecologically relevant differences. Only the fundamental overlap between the species pair, *O. bainae* - *P. ratti* (82%) was greater than 70%. However, the mean realised overlap (55%) between these two species was substantially less than 70%, indicating that these two species interact to separate their niches in individual rats. The distribution of *O. bainae* in experimental infections (Table 3) differed when compared with natural infections (Fig. 1) in that in monospecific infections it occurred in the most anterior segment of the duodenum and this may be due to the absence of competition from *N. magnus* or *P.*

ratti. However, other contributing factors may have been the different species of host, the smaller sample size in experimental infections or the smaller numbers of *O. bainae* in experimental infections.

These observations suggest that the nematode community in *R. fuscipes* is an interactive one. Holmes and Price (1986) separated communities of parasites into two categories, isolationist and interactive, based on their infrapopulations, that is, populations in individual hosts. They suggested that an interactive community has no vacant niches, parasites are not distributed independently and realised distributions of parasites are dependent on other guild members. Some of these features are present in the case of the trichostrongyloid nematode parasites of the bush rat, since the realised overlap was less than the fundamental overlap in most interactions in natural infections.

However, the small intestine of the bush rat does appear to have vacant niches in natural infections, despite the above evidence for an interactive community. Although host immunity may reduce the size of apparent vacant niches (Noble *et al.* 1989) and low transmission rates may prevent parasites filling all available niches (Price 1980), the distribution of the trichostrongyloids in individual rats was independent of nematode numbers. Thus, assuming vacant niches occur, the trichostrongyloids of the bush rat also demonstrate one feature of an isolationist community (Holmes & Price 1986). The "population concentration" and "individual response" hypotheses both explain why the species *N. magnus, O. bainae* and *P. ratti* should occupy distinct niches even when additional vacant niches are available (Holmes & Price 1986). The "population concentration" hypothesis has two components, that narrow niche occupation is essential for the maintenance of intraspecific contact for mating purposes (Rohde 1979, 1982) and that the occupation of discrete niches is important as a

reproductive isolating mechanism preventing hybridization (Sogandares-Bernal 1959; Martin 1969). The "individual response" hypothesis (Price 1984) argues that parasites adapt to the environment they inhabit and consequently fill narrow niches.

The distribution and overlap of trichostrongyloid nematodes in individual bush rats vary greatly from the means but are independent of nematode numbers except in the case of the posterior extent of *O. bainae* in the intestine. The variability in these intracommunities may be due to the biological features of the nematodes and their interactions with one another but may also be caused by variability in the characteristics of the host which influence parasite infracommunities such as host diet (Croll 1976) and blood supply (Croll & Ma 1977). The non-specific host response, pathological responses and acquired immune responses of the host may also influence the distribution of parasites.

The three tichostrongyloid nematode species found in *R. fuscipes* have different biogeographical origins. The genus *Nippostrongylus* occurs primarily in *Rattus* spp. in south-east Asia and in other rodents in Asia and the Middle-East, with a single species in dermopterans (Beveridge & Durette-Desset 1992a). Since the endemic species of *Rattus* in Australia probably reached the continent from south-east Asia (Watts & Aslin 1981), it is likely that *Nippostrongylus* reached Australia with them and that subsequent co-speciation led to the evolution of *N. magnus* in *R. fuscipes* (see Beveridge & Durette-Desset 1992a). The genus *Odilia* occurs primarily in hydromyine or "old endemic" rodents in Australia, principally in the genera *Melomys* and *Uromys*. Species occurring in *Rattus* spp. have been interpreted as transfers from "old endemic" rodents, which probably evolved between 5 and 15 million years ago, to the "new endemic" *Rattus* spp. which have been present on the continent for about 1 million years (Watts & Aslin 1981). Species of *Paraustrostrongylus* occur in possums (Phalangeridae, Petauridae, Burramyidae) and rat kangaroos (Potoroidae) (Spratt *et al.* 1991), with a single species, *P. ratti* in a rodent. The transfer of *Paraustrostrongylus*, and probably *Odilia*, is therefore presumed to be of recent origin (less than 1 million years).

Holmes (1973) suggested that stable communities are older than interactive ones and since most parasite communities are stable, he concluded that they are relatively old. The interactive component of the trichostrongyloid infracommunity in bush rats suggests that it is a comparatively young community. This is consistent with the hypothesis that *P. ratti* and possibly also *O. bainae* are recent invaders. Following their invasion of *R. fuscipes*, *P. ratti* and *O. bainae* have occupied distinctive niches within the new host possibly due to isolationist forces and/or their interactions with the other trichostrongyloid nematode species present in the small intestine. It is possible that *P. ratti* colonised a previously vacant niche at the time of switching since *N. magnus* and *O. bainae* do not occupy this niche even when *P. ratti* is absent.

The other parasites found in the small intestines of bush rats appear to occupy completely different niches from those inhabited by the trichostrongyloid nematodes or to occur at a very low intensity and prevalence (*Capillaria* sp.) and therefore were not considered in the interactions of the trichostrongyloid community in the present study. The distributions of *H. diminuta* and *B. anapolytica* overlapped. However, the two species were never found in the same segment of the small intestine although only two rats were infected with both species. Because of interactions which may occur between them, they may occupy separate niches (Holmes 1973). A larger sample of rats would be needed to examine the extent of interaction between their cestode parasites.

Acknowledgments

References

BEVERIDGE, I. & DURETTE-DESSET, M.-C. (1992a) The morphology of *Nippostrongylus magnus*, a parasite of native Australian rodents. *Trans. R. Soc. S. Aust.* **116**, 109-115.

_____ & _____ (1992b) A new species of trichostrongyloid nematode, *Odilia bainae*, from a native rodent, *Rattus fuscipes* (Waterhouse). *Ibid.* **116**, 123-128.

_____ & _____ (1993) Adult and larval stages of *Paraustrostrongylus ratti* (Nematoda:Trichostrongyloidea) from *Rattus fuscipes*. *Ibid.* **117**, 27-36.

BULL, C. M., BURZACOTT, D. & SHARRAD, R. D. (1989) No competition for resources between two tick species at their parapatric boundary. *Oecologia* **79**, 558-562.

BUSH, A. O. & HOLMES, J. C. (1986) Intestinal helminths of lesser scaup ducks: an interactive community. *Can. J. Zool.* **64**, 142-152.

CHABAUD, A. G. (1965) Spécificité parasitaire pp. 548-557 *In* Grassé, P.-P. (Ed.) "Traité de Zoologie Vol. 4, Classe des Nématodes" (Masson, Paris).

_____ (1982) Spectre d'hôtes et évolution des nématodes parasites de vertébrés. *Mém. Mus. natn. Hist. nat., Paris* **123**, 73-76.

CROLL, N. A. (1976) The location of parasites within their hosts: the influence of host feeding and diet on the dispersion of adults of *Nippostrongylus brasiliensis* in the intestine of the rat. *Int. J. Parasitol.* **6**, 441-448.

_____ & MA, K. (1977) The location of parasites within their hosts: the influence of surgical manipulation of the intestine and mesenteric blood supply on the dispersion of *Nippostrongylus brasiliensis* in the rat. *Ibid.* **7**, 21-26.

DURETTE-DESSET, M.-C. (1985) Trichostrongyloid nematodes and their vertebrate hosts: reconstruction of the phylogeny of a parasitic group. *Advan. Parasitol.* **24**, 239-306.

HOLMES, J. C. (1973) Site selection by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities. *Can. J. Zool.* **51**, 333-347.

_____ & PRICE, P. W. (1980) Parasite communities: the roles of phylogeny and ecology. *Syst. Zool.* **29**, 203-213.

_____ & _____ (1986) Communities of parasites pp 187-213 *In* Anderson, D. J. & Kikkawa, J. (Eds) "Community Ecology: Pattern and Process" (Blackwell Scientific Publications, Oxford).

HURLBERT, S. H. (1978) The measurement of niche overlap and some relatives. *Ecology* **59**, 67-77.

MARTIN, D. R. (1969) Lecithodendriid trematodes from the bat *Peropteryx kappleri* in Colombia, including discussions of allometric growth and significance of ecological isolation. *Proc. Helminthol. Soc. Wash.* **36**, 250-260.

MAWSON, P. M. (1961) Trichostrongyles from rodents in Queensland with comments on the genus *Longistriata* (Nematoda: Heligmosomatidae). *Aust. J. Zool.* **9**, 791-826.

_____ (1973) Amidostomatinae (Nematoda: Trichostrongyloidea) from Australian marsupials and monotremes. *Trans. R. Soc. S. Aust.* **97**, 257-279.

NOBLE, E. R., NOBLE, G. A., SCHAD, G. A. & MACINNIS, A. J. (1989) "Parasitology: the biology of animal parasites." (6th edn.) (Lea & Febiger, Philadelphia).

OBENDORF, D. L. (1979) The helminth parasites of *Rattus fuscipes* (Waterhouse) from Victoria, including description of two new nematode species. *Aust. J. Zool.* **27**, 867-879.

PIANKA, E. R., HUEY, R. B. & LAWLOR, L. R. (1979) Niche segregation in desert lizards pp. 67-115 *In* Horn, D. J., Stairs, G. R. & Mitchell, R. D. (Eds) "Analysis of Ecological Systems" (Ohio State University Press, Columbus).

PRICE, P. W. (1980) "Evolutionary biology of parasites." (Princeton University Press, Princeton, New Jersey).

_____ (1984) Communities of specialists: vacant niches in ecological and evolutionary time pp. 510-523 *In* Strong, D. R., Sinberloff, D. S., Abele, L. & Thistle, A. B. (Eds) "Ecological communities: conceptual issues and the evidence" (Princeton University Press, Princeton, New Jersey).

ROHDE, K. (1979) A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. *Amer. Nat.* **114**, 648-671.

_____ (1982) "Ecology of marine parasites." (University of Queensland Press, St. Lucia).

SCHAD, G. A. (1963) Niche diversification in a parasitic species flock. *Nature* (London) **198**, 404-406.

SOGANDARES-BERNAL, F. (1959) Digenetic trematodes of marine fishes from the Gulf of Panama and Bimini, British West Indies. *Tulane Stud Zool.* **7**, 69-117.

SPRATT, D. M., BEVERIDGE, I. & WALTER, E. L. (1991) A catalogue of Australian monotremes and marsupials and their helminth parasites. *Rec. S. Aust. Mus., Monogr. Ser.* **1**, 1-105.

WATTS, C. H. S. & ASLIN, H. J. (1981) " The Rodents of Australia" (Angus & Robertson, Australia).