Interspecific Interactions among Gastrointestinal Helminths in Pikas of North America

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ABSTRACT: Two helminth communities, comprising seven species in Ochotona princeps and five in O. collaris, were studied for site specificity and interspecific interactions. There were no cases of competitive exclusion, but four species pairs were found concurrently more often than by chance, possibly due to similarities in life cycles. One case of interactive site segregation was demonstrated. There was a high degree of selective site segregation. The pinworm species superficially appeared to overlap, but closer examination demonstrated a migratory phenomenon which concealed a form of site selection related to gut lumen contents in addition to site. An attempt was made to relate the degree of helminth-helminth interaction to the age of the helminth-host association. The communities are old and the component species have therefore been associated for many generations. Only the more recent community members were found to be interactive in their site segregation, indicating that interspecific interactions may play a role in the evolution of site specificity.

INTRODUCTION

Holmes (1973) has put forward a hypothetical evolutionary sequence in which selective site segregation of parasites is derived from interspecific interactions. In this hypothesis, antagonistic interactions result in either competitive exclusion or interactive segregation. Prolonged interactive segregation eventually leads to the evolution of selective segregation, manifested along some axis of the niche such as site or time. Rohde (1976) discounts the effect of interspecific interactions, and suggests that selective site segregation has evolved as a mechanism to bring individuals of the same species together for reproduction. As evidence against Holmes' hypothesis, he points out that monogeneans are as narrowly site-specific in temperate (species-poor) assemblages as they are in tropical (species-rich) ones. Thus, even where there has been little interspecific interaction, there is strong site specificity leaving ample "empty niches."

This paper examines an assemblage of helminths in North American pikas [Mammalia: Ochotona princeps (Richardson) and O. collaris (Nelson)], by comparing the degree or type of interaction between helminth species, to the evolutionary age of the host-helminth association. According to Holmes' hypothesis, those species which have been associated with the host (and therefore with each other) for the longest period should show a high degree of selective site segregation. Conversely, relatively newer acquisitions to the helminth assemblage should interact by either competitive exclusion or interactive site segregation.

COLLECTION METHODS

Necropsies were performed on 102 Ochotona princeps from Alberta and 92 O. collaris individuals from the Yukon Territory of Canada. All pikas were collected by shooting, in Alberta from May to August 1971, and in the Yukon Territory from June to August 1972. Within 5 min of death, the gastrointestinal tract was tied off into sections with cotton thread, in order to prevent postmortem migrations of helminths.

The small intestine was partitioned into approximately eight sections. The anteriormost section was only ca. 3-4 cm in length, while the remaining ones were approximately 15 cm. Some intestines were partitioned into more or less than eight

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sections in the field, and were standardized to eight for the analyses. Thus, each section-type is represented by a different sample size of hosts.

The posterior intestine (caecum and large intestine) was partitioned into three natural zones (see Fig. 1).

Pikas were examined for helminths within 6 hr of death.

**Results**

*Helminths present.*—A total of nine species were found, including one cestode and eight nematodes. Table 1 lists the names of these for each host species. Females of *Cephaluris alaskensis* Akhtar and *C. coloradensis* Olsen were indistinguishable (Hobbs, 1976a), so all individuals of these species were pooled for the majority of the analyses.

*Interactive effects on population size.*—A simple method of testing for competitive exclusion is to compare the frequencies of occurrence of each species of

![Diagram](image)

**Fig. 1.**—Diagrammatic view of the gastrointestinal tract of a pika, showing the sites occupied by helminths encountered in this study

**Table 1.**—List of names of the two helminth communities of pikas

<table>
<thead>
<tr>
<th>Helminth taxon</th>
<th>Host species</th>
<th><em>Ochotona princeps</em></th>
<th><em>Ochotona collaris</em></th>
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<tr>
<td>Phylum Platyhelminthes</td>
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<tr>
<td>Class Cestoda</td>
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<td>Fam. Anoplocephalidae</td>
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<td>Phylum Nematoda</td>
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<td><em>Schizorchis caballeroi</em></td>
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<td>Phylum Nematoda</td>
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<td>Superfam. Trichostrongyloidea</td>
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<td>Fam. Heligmasomidae</td>
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<td>Fam. Trichostrongylidae</td>
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<td></td>
<td><em>Murielus harpespiculus</em></td>
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<td><em>Graphidiella ochotonae</em></td>
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</tbody>
</table>

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all possible pairs of species, in single and concurrent infections. This was done with 2 × 2 chi-square contingency tests (Steel and Torrie, 1960: 371). Juvenile pikas were excluded from these tests because few juveniles were infected with helminths, and their inclusion would have biased the outcome toward positive interaction.

Not one of these tests indicated a significant (i.e., p<0.05) competitive exclusion between species (Fig. 2), but four species pairs were found concurrently more often than by chance. Two others, both involving the genera Cephaluris and Labios- tomomum, were indicative of positive interaction, but were not statistically significant.

![Graph showing interactions between species](image)

**Fig. 2.**—Trellis matrix of 2 × 2 contingency tables for all possible pairs of species. Numbers within each box represent the frequencies of occurrence of each combination. For example, the species Graphidiella ochotonae and Schizorchis caballeroi (upper left-hand box), were found together 39 times, G. ochotonae without S. caballeroi 11 times, S. caballeroi without G. ochotonae 31 times, and neither of these species seven times. The chi-square value is given below each box. All interactions are not significant, except those marked *(p < 0.05), **(p < 0.01), or ****(p <0.005)
In each case, *Labiostomum* was found only in pikas concurrently infected with *Cephaluris*.

Rank correlation is another method of detecting competitive exclusion. It is a little more sensitive than 2 × 2 contingency tests, because it allows for those situations in which competitive exclusion is not absolute; that is, a large population size of species A reduces the numbers of B without completely excluding B. Rank correlations were determined for only those pikas which were infected with at least one species of the pair. Once again, no significant cases of negative interaction were detected with Spearman's rank correlation (Steel and Torrie, 1960: 409). Positive correlations were found between *Cephaluris* spp. and *Eugenurus* species A (p < 0.01), and *Cephaluris* spp. and *Labiostomum coloradensis* Leiby (p < 0.01) in *Ochotona princeps*; and between *Cephaluris* spp. and *Eugenurus talkeetnaeuris* Akhtar (p < 0.01), and *Cephaluris* spp. and *L. rauschi* Akhtar (p < 0.01) in *O. collaris*.

**Interactive site segregation.**—Figure 1 indicates the sites at which helminths of each species are found. Only the pinworms (Oxyuridae) overlap in distribution; more will be said of these later.

The heligmosomid *Murielus harpespiculus* Dikmans is an extreme site specialist occurring almost exclusively in the anterior duodenum within 5 mm of the pyloric sphincter. The cestode *Schizorchis caballeroi*, a site generalist, was not found in this region (Fig. 1). For the analyses, pikas were segregated into three groups, depending upon the population size of *M. harpespiculus*: absent, low (1-10, mean 4.6 worms), and high (1-186, mean 69). Individuals of *S. caballeroi* were categorized by size as: small (up to about 4 mm), or large (4-40 mm). It is uncertain whether or not the small cestodes represent new infections.

Distributions of *Schizorchis caballeroi* under different *Murielus harpespiculus* intensity classes are shown in Figure 3. Differences between these distributions were tested using R × G tests of independence (Sokal and Rohlf, 1969: 509). Results are shown in Table 2.

Although the distributions of each of the two species in single species infections do not overlap, in concurrent infections, *Schizorchis caballeroi* is displaced towards the posterior end of the small intestine. High heligmosomid populations have a significant effect on both large and small cestodes. Low heligmosomid populations do not have a significant effect on the distribution of large cestodes, but are as effective as high populations in altering the distribution of small cestodes.

![Table 2](https://example.com/table2.png)

**Table 2.**—Results of R × C tests of independence between distributions of *Schizorchis caballeroi* along the small intestines of *Ochotona* spp., under different levels of concurrent infection with *Murielus harpespiculus*. The groups Y, A₀, A₁₀, and A₁₁⁺, are as in Fig. 3.
Selective site segregation.—There is a high degree of selective site segregation shown by the helminths of pikas (Fig. 1). The trichostrongyloid nematodes *Graphidiella ochotonae* Olsen and *Murielus harpespiculus* are extreme specialists, and although *Schizorchis caballeroi* is a generalist, it does not overlap with any other species. Unlike the above species, the pinworm nematodes superficially appear to overlap considerably in their site preferences.

In order to test the degree of specialization of the pinworms within the caecum and large intestine, the numbers of each species were recorded for each of the

\[
\begin{align*}
Y & \quad S. \text{ caballeroi in } O. \text{ collaris, not infected with } M. \text{ harpespiculus (} n = 52 \text{ pikas)} \\
A_0 & \quad S. \text{ caballeroi in } O. \text{ princeps, not infected with } M. \text{ harpespiculus (} n = 15 \text{ pikas)} \\
A_{1-10} & \quad S. \text{ caballeroi in } O. \text{ princeps, infected with } 1-10 \text{ M. harpespiculus (} n = 10 \text{ pikas)} \\
A_{11+} & \quad S. \text{ caballeroi in } O. \text{ princeps, infected with } 11-186 \text{ M. harpespiculus (} n = 18 \text{ pikas)}
\end{align*}
\]

![Graph](image_url)

Fig. 3.—Intestinal distributions of small and large *Schizorchis caballeroi* in pikas with different levels of concurrent infection with *Murielus harpespiculus*. Locations of sections 1-7 are shown in Figure 1
three zones in each pika. Each zone has a different internal structure (see Puget and Voisin, 1973, for a detailed description of these structures in Ochotona rufescens). Zone A, consisting of the caecum and a short (10-15 mm) section of large intestine, is thin-walled and has a spiral flap throughout its length, from which extend flat fingerlike processes. The processes are progressively shorter toward the blind end of the caecum. Successive coils of this flap are approximately 5 mm apart. Zone B (=procolon of Kelsall, 1942) is short (15-25 mm), relatively thick-walled and muscular, with reticulate muscle bands. Zone C is thick-walled, glandular, and is folded into three longitudinal lines of transverse pocketlike flaps or haustra.

Pikas, like other lagomorphs, are coprophagous, and excrete two distinct types of feces. Soft feces are loose, have a high water content, are relatively roughage-free, and have the consistency of toothpaste. Soft feces may be reingested by pikas (Tyndale-Biscoe, 1959; Johnson and Maxell, 1966), as in other lagomorphs (Madsen, 1939; Kirkpatrick, 1956; Bookhout, 1959). Hard feces are spherical pellets, ca. 3 mm in diam. They have a relatively high roughage content. Prospective hard feces remain moist and do not form pellets until after passing through Zone C, but because of the relatively high roughage content are easily distinguishable from soft feces in this zone.

Preliminary results of the distribution of pinworms among the three zones during periods of hard feces, and soft feces formation in Zone C have been published (Holmes, 1973); detailed results are shown in Figure 4.

In Ochotona princeps, most individuals of Eugenuris species A are found in Zone A, regardless of the lumen contents of Zone C. When Zone C contained prospective hard feces, individuals of Cephaluris spp. were distributed almost evenly in both A and C, with very few in Zone B. When Zone C contained prospective soft feces, most individuals of Cephaluris spp. were in Zone A. Individuals of Labiostomum coloradensis were found almost exclusively in Zone C, regardless of contents.

In Ochotona collaris, Cephaluris spp. and Labiostomum rauschi had distribution patterns similar to their congeners in Ochotona princeps. Distribution patterns of Eugenuris talkeetnaeus were unlike those of Eugenuris species A, but similar to those of Cephaluris spp. Males of C. alaskensis and C. coloradensis in O. collaris were treated separately (Fig. 4c), but no differences were found ($X^2 = 1.85$; $p > 0.75$; R × C test).

In summary, two species are site-specific in Ochotona princeps and show very little overlap: Eugenuris species A selects Zone A, and Labiostomum coloradensis selects Zone C. Cephaluris spp. are migrators and tend either to avoid prospective soft feces, or select prospective hard feces. One species, L. rauschi, is site-specific in O. collaris, and the other three species are migratory.

**Discussion**

Competitive exclusion and interactive enhancement.—Most of the instances of positive interactions involved pairs of pinworms. According to Gause’s competitive exclusion principle, one might expect strong negative interactions between such closely related species. The question then arises how these species coexist. Following the evolutionary sequence of Holmes (1973), one would predict these species to be segregating resources, either interactively or selectively, such that competition is reduced; this is often the case (see below).

With resource segregation, however, one would still expect only a lack of competitive exclusion, not an interactive enhancement. Occurrence of the latter among pinworms might be due to similarities in life cycle, and environmental requirements outside the host.
Positive interactions have been demonstrated experimentally by Ewing and Todd (1961a and 1961b) for two species of Metastrongylus in swine, and by Colwell and Wescott (1973) and Jenkins (1975) for Nippostrongylus brasiliensis and Nematospiroides dubius in mice. Positive interactions have been observed in field studies, but can often be attributed to mutual requirements at the infective stage, and similarities in life cycle. Thomas (1964) recorded positive relationships between helminth species in brown

**Fig. 4.—Distributions of pinworms in the three zones (A-C, see Fig. 1) of the caecum and large intestine of pikas during periods of hard feces, and soft feces formation. Sample sizes of pinworms (and hosts) are shown below each pie.** (a upper left) pinworms in *Ochotona princeps*, (b upper right) pinworms in *O. collaris* and (c lower) male *Cephaluris alaskensis* and *C. coloradensis* in *O. collaris*.
trout, which he attributed to feeding preferences of the hosts, and Cloutman (1975) reported positive relationships between gill parasites of bass, warmouth and bluegill.

Kisielewska (1970b) reported some interesting examples of positive relationships between helminths in the vole Clethrionomys glareolus (Schreb). She found three positive relationships, all between species occurring in different sites in the host. I reanalyzed her data for two of these associations with $2 \times 2$ chi-square contingency tests, and found only the one involving Heligmosomum halli and Catenotaenia pusilla to be statistically ($p < 0.05$) significant. Kisielewska (1970b) also claimed that while there was a positive interaction for co-occurrence of $H. \text{halli}$ and $C. \text{pusilla}$, there was a negative relationship between intensity of infection of the two species. The figure she refers to for evidence, however (Fig. 2 of Kisielewska, 1970b), does not show any such relationship. Her reasoning requires the assumption of a random distribution of intensity values in single-species infections, a situation she did not encounter except in species with very low prevalence (Kisielewska, 1970a, 1970b). Sample $2 \times r$ chi-square analyses I ran, using data from her figure (1970b, Fig. 2), between intensity frequency distributions of one species under differing intensities of the other, did not show significant effects.

The positive relationships found between pinworm species in pikas of this study could be explained by similarities of life cycle. An experimental study is required to test for more direct relationships between species. Such an approach may prove fruitful for the effect of other species of pinworms on the establishment of Labistomum rauschi and $L. \text{coloradensis}$. No individuals of these species were present in pikas which were not infected with $Cephaluris$ spp., suggesting a successional phenomenon.

Interactive site segregation.—In the well-known interaction of Moniliformis dubius and Hymenolepis diminuta in rats (Holmes, 1961), the specialist ($M. \text{dubius}$) shifts the distribution of the generalist. The system in pikas is similar except that the normal habitat ranges do not overlap. It is unlikely that the two species are competing for a resource, and particularly unlikely that Schizorchis caballeroi could deplete a resource of Murielus harpespiculus, since the latter is upstream. Consequently, there may be no functional significance to the shift. There is another reason for discounting resource competition as a cause. Chappell et al. (1970) observed an anterad migration of $H. \text{diminuta}$ in rats, in response to suboptimal host diets. One might thus expect $S. \text{caballeroi}$ to be found more anterad if $M. \text{harpespiculus}$ were depleting a food resource.

The more common general case of competition involving a specialist and a generalist is niche inclusion, where the niche of the specialist, measured along the resource gradient, is included within the potential niche of the generalist. Competition between such species is theorized to be largely by interference (Case and Gilpin, 1974). Many examples between closely related species of birds, mammals, fishes and arthropods are given by Morse (1974) and Colwell and Fuentes (1975), in which the specialist employs interference competition against the generalist. Although the example in pikas is not niche inclusion, it appears that competition here is interference by the specialist against the generalist. Mechanisms of interference available to parasites may be direct, or indirect via an effect on the host.

The distribution of Schizorchis caballeroi requires further elaboration. It is of interest that small cestodes are situated more anterad than large ones (Fig. 3, Table 2), suggesting a posterior emigration with age. There have been few reports of emigrations in this direction (Crompton, 1973). Rendtorff (1948) showed experimentally that in mice, individuals of the anoplocephalid Atriotaenia symmetrica (Baylis, 1927) Stunkard 1961 shift posterad with age. To my knowledge, my data on the intestinal distribution of $S. \text{caballeroi}$ constitute the only other information of this type for an anoplocephalid. Interpretation of the posterior migration as
age-related is somewhat tenuous, however, because small worms are not necessarily young (Crompton, 1973). Small and immature worms may be that way as a consequence of a crowding phenomenon (Roberts, 1961), or perhaps have destrobilated due to some unknown factor.

Selective site segregation.—Schad (1963) investigated the site selection of eight species of pinworms (Tachygontia) in the colons of tortoises using the technique of quick-freezing the colon immediately after death of the host. He found four pairs of species, each of which had a different longitudinal distribution. He then studied the radial distribution and discovered that one species of each pair tended to be a luminal and the other a paramucosal dweller. In the present study, *Cephaluris* spp. in *Ochotona princeps* overlap with both *Eugenuris* species A and *Labiostomum coloradensis* at different times, but appear to be cueing on properties of the lumen, while the latter species cue on properties of the gut wall. This suggests that *Cephaluris* spp. may be lumen dwellers, and the others paramucosal dwellers.

The situation in *Ochotona collaris* is more puzzling. Not only do both species of *Cephaluris* migrate together, but *Eugenuris talkeetnensis* joins them. Only *Labiostomum rauschi* is sedentary. Perhaps these species are segregated on food preferences. Alternatively, coexistence could occur if each species were principally limited by a different micronutrient, as may be the case for phytoplankton assemblages (Petersen, 1975).

Holmes (1973) and Crompton (1973) have reviewed the literature on helminth migrations. *Hymenolepis diminuta* is known to undergo forward migration in response to food in the host's stomach. Williams et al. (1970) recorded several examples of feeding migration of helminths in rays and cod, and Mackenzie and Gibson (1970) noticed one example in plaice. These examples are perhaps atypical because the fish were brought into the laboratory and starved for some days to bring about a posterior migration. The example in pikas appears to be the first known case of a naturally occurring cyclical migration of a gastrointestinal helminth. Other helminths should be similarly investigated; the phenomenon may be widespread.

Age of host-helminth association.—Helminths of pikas must have had a long evolutionary history together; none of those encountered in this study appears to be new to pikas, as neither the species found nor their congeners are known to occur in hosts other than pikas. The pinworms form a monophyletic group as shown by Hobbs (1976b), and probably are derived from an ancestor common to *Dermatoxys* in leporids.

Among other genera inhabiting pikas in North America, *Graphidiella* does not have close affinities to any living genus, but is probably closest to *Graphidium*, the stomach worm of leporids. The heligmosomid *Murielus* does not have any relatives in the Heligmosomidae, which is now believed to be a polyphyletic group (Durette-Desset, 1971). There are, however, many similarities to the trichostrongylid genus *Nematodirus*, particularly to those species found in leporids (Dikmans, 1939; Durette-Desset, 1974). The cestode *Schizorchis* is the only genus which does not have a counterpart in leporids. Although it must have been in pikas at least before the Illinoian, considering its widespread present distribution in them, it is perhaps the newest of pika helminths. It resembles *Monoeococestus*, parasites of many different groups of mammals in both the Old World and New.

The helminth community system in pikas is therefore an old one. According to Holmes' (1973) hypothesis, individuals in such systems should show an avoidance of competitive exclusion by interactive, and selective segregation. Data given above are consistent with the hypothesis. Indeed, those species which appear to have been in pikas longest (*Graphidiella* and the pinworms) are those which use selective site
segregation, the kind considered by Holmes to be the most highly evolved. Schizorchis, the most recent pika helminth, is most affected by interactive site segregation, as expected.

In conclusion, intraspecific effects such as those given by Rohde (1976) may well be important in the evolution of site specificity in many communities, but interspecific interactions should not be discounted.

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Literature Cited


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