Observations on the Prevalence and Intensity of Capillaria spp. (Nematoda: Trichuroidea) in Wild Carnivora from Ontario, Canada

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ABSTRACT: Four Capillaria spp. were found in eight species of wild Carnivora taken in Ontario, Canada, over a period of 18 months. C. plica was found in raccoons (Procyon lotor), red foxes (Vulpes vulpes), coyotes (Canis latrans), fishers (Martes pennanti), and striped skunks (Mephitis mephitis); C. putorii in short-tailed weasels (Mustela erminea), mink (M. vison), fishers, martens (Martes americana), striped skunks, and raccoons; C. aerophila in red foxes and martens (new host record), and C. procyonis in raccoons and striped skunks.

Data on location within each host species, prevalence, intensity, dispersion, and association are presented. The numerical host-parasite relationships are examined with regard to host species, season, age, and sex. An attempt was made to relate seasonal data with the biology (including feeding habits) of the hosts.

Capillaria aerophila (Creplin, 1839) Travassos, 1915, C. plica (Rudolphi, 1819) Travassos, 1915, C. putorii (Rudolphi, 1819) Travassos, 1915, and C. procyonis Pence, 1975 have been reported from a variety of Carnivora in North America (Law and Kennedy, 1932; Swales, 1933; Read, 1949; Pence, 1975). Unfortunately, most papers concerning Capillaria spp. only contain prevalence data and involve a single host species. Although both prevalence and intensity data are available for C. aerophila and C. plica in foxes (Vulpes vulpes L.) maintained on fur farms (Watkins and Harvey, 1942) little is known about prevalence, intensity, and transmission of Capillaria spp. in populations of wild Carnivora. The population dynamics of any parasite will be affected by the structure of the host community (Holmes, 1979). It is necessary to know the distribution of the parasite within the community of hosts before one can evaluate the population dynamics of any parasite species. Also, in a temperate climate, seasonal changes have the potential to affect the distribution patterns of a parasite within its host populations.

In the present study we examine the numerical host-parasite relationships of four Capillaria species found in wild Carnivora from central southern Ontario, Canada, with reference to species of host, host’s age and sex, and season.

Materials and Methods

Carcasses of wild Carnivora (278) from Ontario, Canada, were obtained directly from trappers or indirectly through the Ministry of Natural Resources during the 1973–1974 and 1974–1975 trapping seasons (Table 1). Some of the animals collected during the spring, summer, and early fall were road kills, others were live trapped using baited No. 11 National (Tomahawk, Wisconsin) traps. Live trapped animals were transported to the laboratory, anesthetized with chloroform and

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killed by intracardiac injection of 1–2 ml of sodium pentobarbitol (Nembutal, Abbott Laboratories).

Species, date, sex, stomach contents and, where possible, age and weight of each animal were recorded. All of the red foxes and most of the raccoons (*Procyon lotor* L.) (*n* = 129 of 140) were aged as juveniles (<1 yr) or adults (>1 yr) by Ontario Ministry of Natural Resources personnel (I. Watt and D. E. Johnston). Red foxes were aged using the cementum annuli technique (Monson et al., 1973) while raccoons were aged using the presence or absence of open root canals and the size of pulp cavities (D. E. Johnston, pers. comm. 1975). Host species other than red fox and raccoon were not aged.

Necropsies were performed as soon after death as possible (48 hr maximum) or the carcasses were frozen (−20° C) until examination. Techniques used for finding and preparing worms for identification are described elsewhere (Butterworth and Beverley-Burton, 1980). Representative specimens have been deposited in the National Museum of Natural Science Collection of Invertebrates (Parasites) Ottawa, Ontario K1A 0M8, Canada (Nos. NMNC (P) 1980-79 to 1980-111), the Commonwealth Institute of Helminthology, 103 St. Peter’s Street, St. Albans, Herts., U.K. (Nos. 3372–3392) and the U.S. National Museum, Parasite Collection, Beltsville, Maryland (Nos. 75693–75702).

Chi-square analyses were used to compare prevalences of *Capillaria* spp. in relation to host, age, and sex. Index of affinity (Fager and McGowan, 1963), and Southwood’s (1966) modification of Whittaker and Fairbanks’ (1958) coefficient of association and the point correlation coefficient (Poole, 1974) were used to analyze association between *Capillaria* spp. Index of affinity was determined by:

\[
I_{AH} = \frac{J}{(N_A N_B)^{\frac{1}{2}}} - \frac{1}{2(N_B)^{\frac{1}{2}}}
\]

where *J* is the number of joint occurrences of species *A* and *B*, and *N_A* and *N_B* are the number of times each species occurred. The point correlation coefficient, also based on presence or absence, was determined by:

\[
V = \frac{ad - bc}{[(a + b)(a + c)(b + d)(c + d)]^{\frac{1}{2}}}
\]

where *a*, *b*, *c*, and *d* correspond to the standard notation of a 2 × 2 contingency table. The coefficient of association was determined by:

\[
I_{ai} = 2 \left[ \frac{J_i}{A + B} - 0.5 \right]
\]

where *J_i* is the number of individuals of *A* and *B* in samples of joint occurrences, and *A* and *B* is the number of individuals of *A* and *B* in all samples.

The following procedures were applied to information collected from raccoons. Worm counts were grouped bimonthly based on the known biology of raccoons. In the present study young raccoons were first collected during July 1974 and the nine bimonthly periods used were as follows: Nov.–Dec. 1973; Jan.–Feb. 1974; Mar.–Apr. 1974; May–June 1974; July–Aug. 1974; Sep.–Oct. 1974; Nov.–Dec. 1974; Jan.–Feb. 1975; Mar.–Apr. 1975. Prevalence is defined as the number (expressed as a percentage) of infected animals in the sample while intensity is the mean number of parasites per infected host. A log_{10} transformation was applied.
to the data to reduce heterogeneity of the variances. Reduction of the heterogeneity of variances was confirmed by Bartlett’s test (Guenther, 1964). A one way analysis of variance and Scheffe’s test were used to compare bimonthly intensity of infection.

Mann-Whitney U (two-tailed) and/or median test (one-tailed) were used to compare intensities of infections between untransformed data groups. $P < 0.05$ was used as the level of statistical significance.

Results

Location

*Capillaria plica* was located almost exclusively in the lumen of the urinary bladder of several host species (Table 1). However, one male from a raccoon was located in the submucosa of the bladder.

*Capillaria putorii* was located in the stomach of raccoons, mink (*Mustela vison* L.), martens (*Martes americana* Turton), fishers (*M. pennanti* Erxleben), striped skunks (*Mephitis mephitis* Schreber), and short-tailed weasels (*Mustela erminea* L.). It was found in the mucus lining the stomach wall and/or in the stomach contents of the host animals. In mink and martens, some worms were found in the lumen of the duodenum.

*Capillaria aerophila* was found within the mucosa of the trachea and bronchi of red foxes and martens. In red foxes most worms (66%) were found in the trachea.

*Capillaria procyonis* was found within the esophageal mucosa of raccoons and skunks.

Prevalence

Prevalences of all four *Capillaria* species are listed in Table 1. Red foxes were only obtainable in October, November, and December 1974 and prevalence of *C. plica* in this host (Table 1) was significantly lower than that in raccoons (84% of 33) collected during the same period. Similarly, mink were only available in winter and no significant difference was found in the prevalences of *C. putorii* in mink (Table 1) and raccoons (70% of 62) collected during the same time period (Nov.–Dec. 1973, 1974; Jan. 1975). Prevalences of *C. aerophila* and *C. procyonis* were not compared between species because host sample sizes were too small for statistical analyses. No significant differences were found between male and female hosts for *C. aerophila*, *C. plica*, and *C. putorii* (Table 1). Prevalences of *C. procyonis* in male and female raccoons were significantly different (Table 1). Prevalences of *C. plica*, *C. putorii*, and *C. procyonis* located in raccoons varied from 25% to 100% and were unrelated to season (Tables 1 and 2).

Prevalences of *C. aerophila* and *C. plica* in juvenile (56% of 27 and 62% of 29, respectively) and adult red foxes (29% of 21 and 42% of 19, respectively) were not significantly different. Prevalences of *C. putorii* and *C. procyonis* in juvenile and adult raccoons were not significantly different (Table 3). Prevalence of *C. plica* in adult raccoons was significantly higher than in juveniles (Table 3). However, considering prevalence only in bimonthly periods in which both juveniles and adults were collected the difference in prevalences was not significant, i.e., adults 62%, juveniles 40%.
Table 1. Occurrence of *Capillaria* spp. in wild Carnivora from Ontario, Canada.

<table>
<thead>
<tr>
<th>Species</th>
<th>Host</th>
<th>No. examined (N)</th>
<th>Prevalence</th>
<th>No. of parasites</th>
<th>Intensity*</th>
<th>Male Prevalence</th>
<th>Male Intensity</th>
<th>Female Prevalence</th>
<th>Female Intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. plica</em></td>
<td>Raccoon†</td>
<td>140‡</td>
<td>58</td>
<td>1-25</td>
<td>4.8 (±5.4)</td>
<td>60</td>
<td>4.9 (±5.8)</td>
<td>56</td>
<td>4.7 (±5.0)</td>
</tr>
<tr>
<td></td>
<td>Red Fox§</td>
<td>48</td>
<td>54</td>
<td>1-14</td>
<td>3.7 (±3.3)</td>
<td>58</td>
<td>3.5 (±3.7)</td>
<td>47</td>
<td>4.1 (±2.6)</td>
</tr>
<tr>
<td></td>
<td>Striped Skunk†</td>
<td>11</td>
<td>18</td>
<td>1</td>
<td>1.0</td>
<td>11</td>
<td>—</td>
<td>11</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Coyote§</td>
<td>6</td>
<td>33</td>
<td>1-3</td>
<td>3.0 (±1.4)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Fisher‡</td>
<td>3</td>
<td>66</td>
<td>1</td>
<td>1.0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>C. putorii</em></td>
<td>Raccoon</td>
<td>138‡</td>
<td>68</td>
<td>1-117</td>
<td>22.0 (±27.7)</td>
<td>74</td>
<td>19.6 (±25.1)</td>
<td>64</td>
<td>26.9 (±30.3)</td>
</tr>
<tr>
<td></td>
<td>Mink†</td>
<td>45</td>
<td>60</td>
<td>1-161</td>
<td>42.0 (±44.9)</td>
<td>33</td>
<td>43.1 (±46.5)</td>
<td>12</td>
<td>31.5 (±39.9)</td>
</tr>
<tr>
<td></td>
<td>Marten†</td>
<td>13</td>
<td>54</td>
<td>1-17</td>
<td>9.8 (±6.3)</td>
<td>67</td>
<td>43.1 (±46.5)</td>
<td>12</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Striped Skunk</td>
<td>11</td>
<td>18</td>
<td>1-9</td>
<td>5.0 (±5.7)</td>
<td>3-8</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Short-tailed Weasel†</td>
<td>10</td>
<td>40</td>
<td>1-10</td>
<td>6.3 (±3.8)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Fisher</td>
<td>3</td>
<td>66</td>
<td>5.5 (±3.8)</td>
<td>3-8</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>C. aerophila</em></td>
<td>Red Fox</td>
<td>48</td>
<td>44</td>
<td>1-8</td>
<td>2.7 (±1.9)</td>
<td>31</td>
<td>3.4 (±2.1)†</td>
<td>17</td>
<td>1.5 (±0.5)†</td>
</tr>
<tr>
<td></td>
<td>Marten</td>
<td>13</td>
<td>15</td>
<td>1</td>
<td>1.0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>C. procyonis</em></td>
<td>Raccoon</td>
<td>129‡</td>
<td>59</td>
<td>1-15</td>
<td>4.3 (±3.2)</td>
<td>73</td>
<td>4.2 (±3.2)§</td>
<td>56</td>
<td>4.5 (±3.6)</td>
</tr>
<tr>
<td></td>
<td>Striped Skunk</td>
<td>11</td>
<td>18</td>
<td>5.5 (±3.5)</td>
<td>3-8</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

* Mean (±standard deviation).
† Central southern Ontario—including the counties of Huron, Wellington, and Waterloo.
§ Total number of raccoons examined was 140: 2 stomachs were damaged and are excluded as were 11 oesophagi from raccoons examined prior to the initial finding of *C. procyonis*.
‡ Central southern Ontario—including the counties of Huron, Middlesex, Perth, and southern Bruce.
§ Central Ontario—District of Parry Sound.
¶ Significant difference at 95% level.
Table 2. Occurrence of *Capillaria plica*, *C. putorii*, and *C. procyonis* in raccoons (*Procyon lotor*) from central southern Ontario.

<table>
<thead>
<tr>
<th>Months</th>
<th>No. examined</th>
<th>Prevalence (%)</th>
<th>Intensity (± 1 SD)</th>
<th>Var. mean</th>
<th>No. examined</th>
<th>Prevalence (%)</th>
<th>Intensity (± 1 SD)</th>
<th>Var. mean</th>
<th>No. examined</th>
<th>Prevalence (%)</th>
<th>Intensity (± 1 SD)</th>
<th>Var. mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nov.–Dec. 1973</td>
<td>30</td>
<td>40</td>
<td>1.7 ± 0.9</td>
<td>0.9:1</td>
<td>30</td>
<td>53</td>
<td>6.3 ± 7.1</td>
<td></td>
<td>8.1:1</td>
<td>23</td>
<td>48</td>
<td>2.6 ± 1.6</td>
</tr>
<tr>
<td>Jan.–Feb. 1974</td>
<td>21</td>
<td>57</td>
<td>1.8 ± 1.3</td>
<td>1.0:1</td>
<td>21</td>
<td>48</td>
<td>6.5 ± 6.8</td>
<td></td>
<td>7.0:1</td>
<td>21</td>
<td>48</td>
<td>2.1 ± 2.1</td>
</tr>
<tr>
<td>Mar.–Apr. 1974</td>
<td>5</td>
<td>100</td>
<td>1.4 ± 0.9</td>
<td>0.6:1</td>
<td>5</td>
<td>40</td>
<td>8.5 ± 10.6</td>
<td></td>
<td>13.2:1</td>
<td>5</td>
<td>60</td>
<td>4.3 ± 4.9</td>
</tr>
<tr>
<td>May–Jun. 1974</td>
<td>11</td>
<td>64</td>
<td>6.6 ± 6.7</td>
<td>6.8:1</td>
<td>10</td>
<td>80</td>
<td>35.4 ± 33.7</td>
<td></td>
<td>32.0:1</td>
<td>8</td>
<td>25</td>
<td>1.5 ± 0.7</td>
</tr>
<tr>
<td>Jul.–Aug. 1974</td>
<td>18</td>
<td>56</td>
<td>6.5 ± 5.9</td>
<td>5.4:1</td>
<td>18</td>
<td>72</td>
<td>25.9 ± 30.9</td>
<td></td>
<td>36.8:1</td>
<td>18</td>
<td>39</td>
<td>3.4 ± 2.0</td>
</tr>
<tr>
<td>Sep.–Oct. 1974</td>
<td>16</td>
<td>81</td>
<td>5.7 ± 5.3</td>
<td>4.8:1</td>
<td>16</td>
<td>88</td>
<td>26.4 ± 23.2</td>
<td></td>
<td>20.4:1</td>
<td>16</td>
<td>56</td>
<td>5.9 ± 4.2</td>
</tr>
<tr>
<td>Nov.–Dec. 1974</td>
<td>22</td>
<td>77</td>
<td>8.5 ± 7.0</td>
<td>5.9:1</td>
<td>21</td>
<td>90</td>
<td>41.6 ± 38.1</td>
<td></td>
<td>34.8:1</td>
<td>21</td>
<td>86</td>
<td>5.9 ± 3.8</td>
</tr>
<tr>
<td>Jan.–Feb. 1975</td>
<td>10</td>
<td>30</td>
<td>2.7 ± 2.1</td>
<td>1.6:1</td>
<td>10</td>
<td>90</td>
<td>10.6 ± 14.5</td>
<td></td>
<td>19.9:1</td>
<td>10</td>
<td>90</td>
<td>4.1 ± 2.5</td>
</tr>
<tr>
<td>Mar.–Apr. 1975</td>
<td>7</td>
<td>27</td>
<td>1.5 ± 0.7</td>
<td>0.3:1</td>
<td>7</td>
<td>57</td>
<td>13.5 ± 7.2</td>
<td></td>
<td>3.9:1</td>
<td>7</td>
<td>100</td>
<td>5.9 ± 3.3</td>
</tr>
</tbody>
</table>

* Solid lines indicate no significant difference between bimonthly period. Difference between groups (1 and 2) was significant at 95% level.
Table 3. Occurrence of *Capillaria plica*, *C. putorii*, and *C. procyonis* in juvenile and adult raccoons (*Procyon lotor*) from central southern Ontario.

<table>
<thead>
<tr>
<th>Months</th>
<th>Juvenile</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Prevalence (%)</td>
<td>Intensity (± 1 SD)</td>
</tr>
<tr>
<td><em>Capillaria plica</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nov.–Dec. 1973</td>
<td>17 / 24</td>
<td>1.5 ± 0.6</td>
</tr>
<tr>
<td>Jan.–Feb. 1974</td>
<td>10 / 40</td>
<td>1.0 ± —</td>
</tr>
<tr>
<td>Mar.–Apr. 1974</td>
<td>1 / —</td>
<td>1.0 ± —</td>
</tr>
<tr>
<td>May–Jun. 1974</td>
<td>0 / —</td>
<td>— ± —</td>
</tr>
<tr>
<td>Jul.–Aug. 1974</td>
<td>5 / 0</td>
<td>— ± —</td>
</tr>
<tr>
<td>Sep.–Oct. 1974</td>
<td>10 / 70</td>
<td>6.1 ± 6.2</td>
</tr>
<tr>
<td>Nov.–Dec. 1974</td>
<td>6 / 50</td>
<td>4.0 ± 2.7</td>
</tr>
<tr>
<td>Jan.–Feb. 1975</td>
<td>4 / 25</td>
<td>5.0 ± —</td>
</tr>
<tr>
<td>Mar.–Apr. 1975</td>
<td>0 / —</td>
<td>— ± —</td>
</tr>
<tr>
<td>Total*</td>
<td>53 / 38†</td>
<td>3.6 ± 4.3</td>
</tr>
</tbody>
</table>

*Capillaria putorii*  
Nov.–Dec. 1973 17 / 53 4.1 ± 5.0 9 / 78 9.0 ± 8.8  
Jan.–Feb. 1974 10 / 40 5.3 ± 6.6 9 / 67 7.3 ± 7.4  
Mar.–Apr. 1974 1 / — 1.0 ± — 3 / 0 — —  
May–Jun. 1974 0 / — — — 10 / 80 39.6 ± 33.9  
Jul.–Aug. 1974 5 / 40 1.5 ± 0.7† 13 / 85 30.4 ± 31.7†  
Sep.–Oct. 1974 10 / 80 22.8 ± 29.2 5 / 100 30.0 ± 13.8  
Nov.–Dec. 1974 5 / 80 35.3 ± 24.6 7 / 71 17.8 ± 12.6  
Jan.–Feb. 1975 4 / 100 6.3 ± 5.9 6 / 83 14.0 ± 19.0  
Mar.–Apr. 1975 0 / — — — 7 / 57 13.5 ± 7.2  
Total 52 / 62 12.8 ± 20.1† 69 / 74 21.9 ± 27.7†  

*Capillaria procyonis*  
Nov.–Dec. 1973 15 / 60 2.7 ± 1.7 6 / 17 4.0 —  
Jan.–Feb. 1974 10 / 40 1.8 ± 0.5 9 / 44 3.0 ± 3.4  
Mar.–Apr. 1974 1 / 100 2.0 ± — 3 / 33 1.0 —  
May–Jun. 1974 0 / — — — 8 / 25 1.5 ± 0.7  
Jul.–Aug. 1974 5 / 0 — — 13 / 62 3.5 ± 3.9  
Sep.–Oct. 1974 9 / 44 7.5 ± 5.8 5 / 80 3.8 ± 1.7  
Nov.–Dec. 1974 5 / 100 7.2 ± 4.9 7 / 57 5.0 ± 3.6  
Jan.–Feb. 1975 4 / 100 4.3 ± 2.2 6 / 83 4.0 ± 3.0  
Mar.–Apr. 1975 0 / — — — 7 / 100 5.9 ± 3.3  
Total 49 / 53 4.4 ± 3.8 64 / 56 4.0 ± 2.8  

* Ages available for 129 of 140 raccoons.  
† Significant difference ± 95% level.

**Intensity**

Intensities of all four species of *Capillaria* are listed in Table 1. Intensity of *C. plica* in raccoons (7.5 ± 6.5 (mean ± 1 SD) was significantly higher than intensity in red foxes (Table 1) collected during the same period (Oct.–Dec. 1974). Intensity of *C. putorii* in mink (Table 1) was significantly higher than in raccoons (21.9 ± 30.9) collected during the same time periods (Nov.–Dec. 1973, 1974; Jan. 1975).

Intensities of *C. aerophila* in male and female red foxes were significantly
different (Table 1). Comparison of intensities of other Capillaria spp. indicated no significant differences between male and female hosts (Table 1).

Intensities of C. aerophila and C. plica were not significantly different between juvenile (2.7 ± 2.1 and 4.1 ± 3.8, respectively) and adult (2.7 ± 1.6 and 2.9 ± 1.8, respectively) red foxes. Combined intensity from all bimonthly periods of C. _putorii_ in adult raccoons was significantly higher than in juveniles (Table 3), although when juveniles born in 1974 were compared to adults during the same periods (Jul. 1974–Feb. 1975) the difference was not significant. Combined intensities from all bimonthly periods of _C. plica_ and _C. procyonis_ in juvenile and adult raccoons were not significantly different (Table 3).

Significant differences in intensity between bimonthly periods were found in both _C. plica_ and _C. putorii_ in raccoons. However, no significant differences were found between intensities of _C. procyonis_ during the same periods (Table 2). Both _C. plica_ and _C. putorii_ had significantly higher intensities during spring, summer, and fall (May–Dec. 1974) than in winter (Jan.–Apr. 1974, 1975) (Table 2; Fig. 1). The decrease in intensity of _C. putorii_ during the summer and early fall of 1974 was not significant (Table 2). Intensities of both _C. plica_ and _C. putorii_ were significantly higher in Nov.–Dec. 1974 than in the same period in 1973 (Table 2). Intensity of _C. putorii_ in adult raccoons reached their highest value in spring (39.6) and remained high until early fall (30.0), decreasing in late fall (17.8), whereas intensity in juvenile raccoons increased from its lowest value in summer (1.5) to its highest value in late fall (35.3) (Table 3). Adult raccoons had a significantly higher intensity of _C. putorii_ than juveniles during July–August.

Figure 1. Changes in intensity of infection of _Capillaria plica_, _C. putorii_, and _C. procyonis_ in raccoons (Procyon lotor) collected from central southern Ontario during the months November 1973 to April 1975.
Figure 2. Frequency distribution of numbers of Capillaria plica in raccoons (Procyon lotor) collected from central southern Ontario during periods of low and high intensity.

1974. All other bimonthly comparisons of intensities of Capillaria spp. between juvenile and adult raccoons were not significant (Table 3).

Dispersion

Frequency distributions of C. aerophila and C. plica in red foxes and C. plica, C. putorii, and C. procyonis in raccoons were overdispersed. Generally, C. plica, C. putorii, and C. procyonis in raccoons had the largest variance to mean ratios (var.:mean > 1) during periods of high intensity (Table 2). Figures 2 and 3 indicate the change in the distribution of C. plica and C. putorii in the host population during periods of high and low intensity.

Association

Capillaria aerophila and/or C. plica occurred in 66% of the red foxes examined. The two species occurred concurrently in 13 of 46 (28%) red foxes. The number of concurrent infections was not significant.

* A total of 50 red foxes was examined, two had damaged urinary bladders and two had damaged tracheae, all four were excluded from analyses.
Figure 3. Frequency distributions of numbers of *Capillaria putorii* in raccoons (*Procyon lotor*) collected from central southern Ontario during periods of low and high intensity.

One or more of *C. procyonis*, *C. putorii*, and *C. plica* occurred separately or concurrently in 133 of 140 (95%) raccoons examined. *C. procyonis*, *C. putorii*, and *C. plica* occurred concurrently in 46 (36%) raccoons; *C. procyonis* and *C. putorii* in 61 (48%) raccoons; *C. procyonis* and *C. plica* in 51 (40%) raccoons; and *C. putorii* and *C. plica* in 63 (46%) raccoons. The number of concurrent infections of *C. procyonis* and *C. putorii* and concurrent infections of *C. putorii* and *C. plica* were significant while concurrent infections of *C. procyonis* and *C. plica* were not.

The numbers of concurrent infections of *C. procyonis*, *C. putorii*, and *C. plica* in raccoons were examined during the five bimonthly periods of low intensity (Nov. 1973–Apr. 1974; Jan.–Apr. 1975) and the four periods of high intensity (May–Dec. 1974). During periods of low intensity the number of concurrent infections involving all three species (15 [27%]) or even pairs of species was not significant (Table 4). In comparison, during periods of high intensity the number of concurrent infections involving all three species (31 [50%]) was significant as was the number of concurrent pairs of species (Table 4).
Table 4. Concurrent pairs, ‘Index of Affinity (I_{AB})’, ‘Point Correlation Coefficient (V)’, and Coefficient of Association (I_{ai}) as measures of association of concurrent infections between C. plica, C. putorii, and C. procyonis in raccoons (Procyon lotor) from central southern Ontario.

<table>
<thead>
<tr>
<th>Species</th>
<th>Concurrent pairs</th>
<th>(I_{AB})</th>
<th>Point correlation coefficient (V)</th>
<th>(I_{ai})</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low intensity</td>
<td>High intensity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capillaria procyonis</td>
<td>26 (39%)</td>
<td>35 (57%)*</td>
<td>0.74</td>
<td>0.43</td>
</tr>
<tr>
<td>Capillaria putorii</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capillaria procyonis</td>
<td>20 (30%)</td>
<td>31 (49%)*</td>
<td>0.69</td>
<td>0.36</td>
</tr>
<tr>
<td>Capillaria plica</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capillaria putorii</td>
<td>21 (29%)</td>
<td>42 (65%)*</td>
<td>0.79</td>
<td>0.46</td>
</tr>
</tbody>
</table>

* Significant difference at 95% level.

Index of affinity (I_{AB}) and point correlation coefficient (V) indicated a positive association in concurrent pairs during periods of high intensity (Table 4). In addition, the coefficient of association (I_{ai}) indicated high numbers of individuals occur most often in concurrent infections of C. putorii and C. plica (Table 4).

Levels of intensity of individual species, during periods of high intensity, were not significantly different in the presence or absence of other species with the exception of C. putorii. Levels of intensity of C. putorii were significantly higher in the presence of C. plica as compared to levels of intensity when C. plica was absent. In addition, rank correlations (Kendall’s tau) indicated, during periods of high intensity, only C. putorii and C. plica varied significantly in concert.

**Discussion**

*Capillaria* spp. in Carnivora are widely distributed over North America (Law and Kennedy, 1932; Swales, 1933; Harkema and Miller, 1964; Miller and Harkema, 1964, 1968; Dorney and Lauereman, 1968; Holmes and Podesta, 1968; Pence, 1975; Smith, 1978).

Of the species observed in the present study C. aerophila, C. plica, and C. putorii have been found in their respective hosts over most of the holarctic region but C. procyonis has been reported only from North America where raccoons appear to be the natural definitive host. It is interesting that no *Capillaria* spp. have been reported from raccoons introduced into the Soviet Union (Aliiev and Sanderson, 1966). C. aerophila and C. plica both occur in red foxes throughout most of its distribution (Skrjabin et al., 1957). In our study area, C. plica was found with a high prevalence in both raccoons and red foxes. Intensity and prevalence were both significantly higher in raccoons than in red foxes leading to the conclusion that raccoons are the required definitive host (sensu Holmes, 1979) in southern Ontario. However, this must be interpreted with caution as we lack information regarding the relative host population densities needed to make this conclusion (Holmes et al., 1977). Also, little is known about the behavior of these two nocturnal animals (Ables, 1975; Fritzell, 1978) and it is impossible to determine if the populations of C. plica in raccoons and red foxes are of mixed or separate origin. In the present study C. putorii was found in raccoons, skunks, weasels, martens, and mink. Elsewhere it occurs extensively in a variety of mustelid hosts (Skrjabin et al., 1957) and the European hedgehog (*Erinaceus europaeus*) (Skrjabin et al., 1957; Fahmy, 1964). C. putorii in raccoons shows con-
sistent morphological differences from specimens collected from mustelid hosts (Butterworth and Beverley-Burton, 1980). The morphological differences could indicate a genetic drift between the two populations, one in raccoons and the other in mustelids.

Depending on the species of Capillaria involved the life cycle may be monoxenous or heteroxenous. Eggs are passed in the feces or urine of the definitive host and embryonate in the external environment. C. aerophila and C. plica have been shown to use “earthworms” as intermediate hosts (Borovkova, 1941 (in Rysavy, 1969); Petrov and Borovkova, 1942; Enigk, 1950). C. putorii may be transmitted directly by ingestion of larvated eggs or indirectly by ingestion of oligochaetes containing larvae (Skarbilovich, 1945).

Significant differences in prevalence and intensity of C. plica and C. aerophila and the age of red foxes were not found in our study. However, differences between juveniles and adults in intensity of C. plica and C. aerophila have been reported by Watkins and Harvey (1942) who found juvenile foxes with a higher intensity, of both C. aerophila and C. plica, than adult foxes. This difference may relate to the higher frequency of occurrence of earthworms in the diet of juvenile red foxes compared to adults (Burrows, 1968; Jefferies, 1974; Richards, 1977). The reasons for a lower intensity of C. aerophila in female foxes than in males is unknown. Any behavioral difference would also be expected to affect the intensity of C. plica as well, unless dispersion of the species, one in the urine and the other in the feces is a major factor.

The significant difference in prevalence of C. procyonis in male and female raccoons is difficult to explain because the life cycle is unknown. Female raccoons are reported to have a smaller home range than male raccoons (Cowan, 1973; Fritzell, 1978). However, if home range size was important in determining prevalence of C. procyonis one might expect it to be important for all three Capillaria species.

In an environment with a seasonal climatic variation there will often be fluctuations in resource availability. These fluctuations have the potential of altering transmission patterns between hosts and their parasites. Oligochaetes (lumbricids) are reported to show differences in activity and population numbers related to seasonal climatic patterns (Edwards and Lofty, 1972). Both activity and population numbers increase as soil temperature and moisture increase (Gerard, 1967; Edwards and Lofty, 1972; Nordström, 1975) and, according to Gerard (1967) most oligochaetes reach a peak in activity and numbers in summer and fall unless conditions are dry. In addition, the daily activity pattern of oligochaetes is affected by light, temperature, and moisture: during periods of low light intensity (night), rainfall or heavy dew and soil temperatures of greater than 5°C, surface activity increases (Svendsen, 1957; Gerard, 1967). The variations of intensity of C. plica and C. putorii in raccoons in bimonthly periods probably reflect seasonal changes in the activity of both oligochaetes and raccoons.

Raccoons mate from January to April, with maximum mating activity from mid-January to mid-March. The gestation period lasts approximately 63 days and the young remain in the den for approximately 2 mo (Johnson, 1970; Sanderson and Nalbandov, 1973). Raccoons enter dens and movement is minimal during winter when temperatures fall below 0°C (Steuwer, 1943; Cowan, 1973). In the present study young raccoons were first collected during July 1974. The lowest
intensity of *C. putorii* was during the winter months (January to April) and the highest was during the spring (May–June) and fall (September–December). The increase in activity of raccoons in spring after winter denning appears to correspond with the spring increase of *C. putorii*. The slight decrease in intensity of *C. putorii* in summer (July–August) was associated with the presence of juvenile raccoons in the population with a significantly lower intensity. Most young raccoons leave the den and are weaned in July (Schneider et al., 1971; Cowan, 1973).

The intensity of *C. plica* did not decrease during the summer as did *C. putorii*. Juvenile raccoons examined in summer were uninfected with *C. plica* suggesting there was no transmission in the den. The presence of *C. putorii* in some juveniles during summer and not *C. plica* is possibly related to the shorter prepatent period (26–32 days) of *C. putorii* (Skarbilovich, 1945) than that of *C. plica* (58–63 days) reported by Enigk (1950).

Intensities of *C. plica* and *C. putorii* were higher in the fall of 1974 than those observed in the fall of 1973. One explanation for this difference is that conditions were less dry during the summer and early fall of 1974 compared to the same periods in 1973 (in July, August, and September, 1973 there were 17 days of precipitation >0.01 mm while in 1974 there were 30) (Canadian Department of Environment, Atmospheric Environment, Monthly Records, Meteorological Observations in Canada. 1973, 1974). The greater precipitation in 1974 may have provided increased opportunity for raccoons to feed on oligochaetes as seven raccoons, taken during the period July to September 1974, had oligochaete remains in their stomachs and two of these contained over 100 earthworms. In contrast, oligochaetes were not found in the stomach contents of raccoons during any other period.

Intensity of *C. procyonis* did not vary seasonally. Several explanations are possible: the host is being continually reinfected, the longevity of the worms is such that overlapping generations may mask seasonal fluctuations, the larval stages may reflect seasonal changes in transmission which were not detected, or a density-dependent mechanism may be operating to limit numbers.

Frequency distributions of all species were overdispersed (variance/mean > 1). An overdispersed distribution indicates an unequal chance of infection for all hosts, but whether this is a result of an aggregated distribution of intermediate stages or hosts, or variance in host susceptibility is unknown.

Caution must be exercised when methods or interpretations of association analysis are chosen. Good reviews of the methods and possible interpretations are presented by Fager (1957) and Goodall (1978). Association analyses (chi-square, index of affinity, point correlation) based on presence or absence only, indicated a positive association between all three species during periods of high intensity. The lumping of individuals in joint occurrences (Whittaker and Fairbanks' (1958) equation) also indicated a positive association. However, rank correlation indicated only *C. putorii* and *C. plica* varied in concert. Lumpning of data over the entire period masked the difference in association between species in periods of high and low intensity. Analysis based on presence or absence of a species may simply reflect the utilization of the host involved, by the parasite, and not reflect any relationship between *Capillaria* species. The positive association found between *C. plica*, *C. putorii*, and *C. procyonis* during periods of high intensity may simply reflect the importance of this period in the transmission of the parasite to
the definitive host. The positive association between the number of worms of \textit{C. plica} and \textit{C. putorii} may reflect the utilization of oligochaetes by both species and a similar seasonal transmission pattern.

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**Literature Cited**


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