Journal of the Minnesota Academy of Science

Volume 47 | Number 1 Article 4

1981

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Alternative Hypotheses on Ecological Effects of Meningeal Parasite (Parelaphostrongylus tenuis)

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ABSTRACT — *P. tenuis* is a ubiquitous parasite of white-tailed deer *(Odocoileus virginianus)* that can cause mortality in woodland caribou *(Rangerifer tarandus)* and moose *(Alces alces)*. A hypothesis that *P. tenuis* prevents overlapping distributions of these species in southern boreal regions was inconsistent with distribution records. A revised hypothesis that *P. tenuis* does not prevent overlapping distributions if deer exist at natural densities was consistent with these records but did not state the parasite's ecological effects. A hypothesis that *P. tenuis* allows deer to outcompete woodland caribou or moose on portions of natural environments or in man-modified environments where deer densities are relatively high appeared to be consistent with published accounts of mortality from the parasite and other reviewed literature. Thus, statements that *P. tenuis* either does or does not prevent or restrict overlapping distributions of woodland caribou or moose with white-tailed deer need to be further qualified.

Parelaphostrongylus tenuis is a non-host specific parasite of white-tailed deer (Anderson 1972, Lankester *et al.* 1976). Infection is by accidental ingestion of terrestrial gastropods which are an intermediate host for the parasite's larval stages. This parasite does not appear to cause significant mortality in white-tailed deer. It is known to cause mortality in experimentally infected woodland caribou and moose calves (Anderson and Strelive 1968, Anderson 1964) and in a woodland caribou placed on an island populated with white-tailed deer (Behrend and Witter 1968), in woodland caribou placed in a fenced enclosure with high densities of deer (Trainer 1973), in moose in the wild (Anderson 1965) and in European reindeer (*R. t. tarandus)* placed on an island with deer (Anderson 1971).

From the mortality of experimentally infected woodland caribou and reindeer introduced onto an island with white-tailed deer, Anderson (1972) predicted that it will not be possible to reintroduce caribou into areas where deer have a high prevalence of *P. tenuis.* Trainer (1973) believed that his unsuccessful introductions of caribou into an enclosure with high deer densities supported this prediction. Both authors also suggested the possibility that the parasite was a factor in the declines of woodland caribou on the southern portions of their range. Others (Smith 1940, Cringen 1957, Bergerud 1974, Benson and Dodds 1977) have attributed declines to excessive hunting in combination with habitat changes or increases in predators or deer with *P. tenuis.* Evidence that reintroductions of caribou can fail in habitats where moose still occur, but deer with *P. tenuis* became abundant, is presented by Dauphine (1975).

Moose - Deer relationships examined

Trainer (1973) reports that introductions of moose into an enclosure with high densities of deer with *P. tenuis* also failed. Others (Karns 1967, Telfer 1967, Behrend and Witter 1968, Kelsall and Prescott 1971, and Gilbert 1974) have attributed decreases or increases in free-ranging moose to corresponding increases or decreases in deer densities. However, several of these authors and Kearney and Gilbert (1976) also present evidence that differences in habitat use by time and/or area allow moose and deer with *P. tenuis* to be sympatric species.

Woodland caribou, moose, white-tailed deer and elk *(Cervis elaphus)* were all present before and during the early stages of settlement and logging in the Voyageurs National Park area (Cole 1979). Extripations of caribou and elk and declines of moose to remnant numbers by the early 1920's were associated with hunting which provisioned early settlements, logging camps, and homesteads. However, over a 1907 to 1039 period when the area's forests were first logged (Rakestraw *et al.* 1979) deer increased from relatively low densities (possibly less than 2/km^2) to high densities of 8 or more/km^2 as reported by Erickson *et al.* (1961). Declines back to low densities occurred despite the absence of other cervid competitors (moose remain a non-viable remnant) and were mainly associated with maturing forests.

Another possible interpretation from the literature reviewed thus far is that the mortality of caribou or moose from *P. tenuis* results from density-influenced interspecific competition. Such competition characteristically prevents competitors of a species from appropriating the portions of an environment (or niche) where the species has a competitive advantage (Miller 1967). Competition usually maintains the densities and distributions of competing species in some dynamic equilibrium, but can contribute to complete or partial replacements if changes due to climate or man favor one species over another. The validity of this and alternative interpretations are explored in the following section.

Approaches to testing alternative hypotheses

Hypotheses about complex ecological relationships can be easily deduced but are difficult to test in the laboratory or field. An approach described by Poore (1962) involves testing a stated hypothesis by systematically seeking information to show it is false. Any inconsistent information requires that a hypothesis be rejected and restated for consistensy with all information. Repeated rejections and restatements ultimately result in a refined hypothesis that is consistent with a broad base of reference information and less likely to be false.

Some interpretations about *P. tenuis,* in the form of testable hypotheses, follow. These assume the parasite is ubiquitous in white-tailed deer and transmissions are mainly

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functions of deer and other cervid densities and distributions. They only apply to large areas of mainland, southern boreal forest vegetation, and not to islands that lack sufficient space or hab itat diversity to accommodate species with overlapping requirements. Deer densities are assumed to be usually less than 2 per km^2 under natural conditions, and to increase three-fold or more in man-modified environments.

1. ***P. tenuis* prevents overlapping distributions of woodland caribou and/or moose with white-tailed deer.**
2. ***P. tenuis* does not prevent overlapping distributions of woodland caribou and/or moose with white-tailed deer, if deer occur at natural densities.**
3. ***P. tenuis* allows white-tailed deer to outcompete woodland caribou and/or moose on the portions of natural boreal forest environments where deer densities are highest (e.g. winter or spring concentration areas).**

The first hypothesis paraphrases interpretations from some of the early literature on *P. tenuis.* It must now be rejected because it is inconsistent with additional evidence that white-tailed deer either had or still have overlapping distributions with woodland caribou and moose in some southern boreal forest regions. Hall and Kelson (1959) show the original distributions of all three species overlapped along the southern boundary of boreal forest communities (Whitaker 1970). Reports by Curry-Lindahl and Harroy (1972), Freddy and Erickson (1975) and Stardom (1975) show all three still coexist in several Canadian and one adjoining U.S. area, but it is not certain that *P. tenuis* is present in all of these locations (Anderson 1972). However, records of commercial sales of meat of caribou, moose and white-tailed deer in a 1894-1901 gold-rush settlement (Treuer 1979) and detailed accounts of hunting all three species in a 1889-1901 diary by E.L. Brown (Unpub. transcription, Minnesota Historical Society) tend to establish that all were present in northern Minnesota before the natural vegetation was changed by logging.

The second hypothesis that *P. tenuis* does not prevent overlapping distributions if deer occur at natural densities is a rephrasing of the first so it is consistent with species distribution records. It is also consistent with the reviewed papers that show differences in species densities or distributions, by time or area, allow coexistence of deer with *P. tenuis* and moose. Similar relationships can be predicted for deer and caribou. This prediction could be tested by reintroducing caribou into southern boreal environments where deer with *P. tenuis* occur at natural densities.

The third hypothesis (*P. tenuis* allows deer to outcompete caribou and/or moose on portions of areas where deer densities are highest) predicts the actual ecological effects of this parasite in a relatively stable southern boreal environment. Environmental changes from natural or human influences could result in more or less competition and corresponding changes in species distributions and densities. This hypothesis seems consistent with species distribution records, the literature which shows *P. tenuis* can cause mortality in caribou or moose, and the accumulated evidence that such mortality can be a function of both densities and distrib utions of deer. It is also consistent with an abundant literature which shows that species with partly overlapping requirements must compete or interfere with each other to coexist. This literature is reviewed by Allee *et al.* (1949) and Miller (1967).

Both tentative conclusions may be correct

As is often the case in biology, conclusions which appear to be conflicting are both correct, but for different situations. In man-modified environments that support higher-than-natural deer densities, *P. tenuis* can prevent or restrict caribou and moose from having overlapping distributions with deer. In natural southern boreal environments that support low deer densities, *P. tenuis* does not prevent overlapping distributions and may actually allow deer to coexist with caribou or moose. A recently discovered ubiquitous parasite *(Elaphostrongylus cervi)* in woodland caribou (Lankester *et al.* 1976) may similarly prevent moose, and possibly other cervids, from excluding caribou from their particular niche in southern boreal environments. Such relationships, where a non-specific parasite provides its usual host with a competitive advantage, are probably common in mixed species systems and an important contribution to species diversity. Further tests of the hypotheses developed here are encouraged.

ACKNOWLEDGEMENTS

M. Lankester and T.C. Dauphine and P.D. Kerns reviewed an early draft of the paper and made helpful suggestions. Any errors of interpretation in the final paper are mine.

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Faculty members of St. Cloud State University: John Coulter, Hugh Barker, Nohammed Bahauddin, Wayland Ezell, Michael Garrity, Alexander MacWilliams, John Carpenter, Donald Peterson, Leonard Soroka, Science Fair Coordinator; David F. Grether, Science Fair Finance Chairman.

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Although Spring and Fall membership meetings are the most visible activities of the Minnesota Academy of Science, two functions directed to young and future scientists have achieved increasing attention in recent years.

An annual Junior Science, Engineering, and Humanities Symposium gives selected high school and junior high students opportunities to present and share research papers and projects with their youthful contemporaires over a wide area. Starting with local programs, outstanding students can move through statewide, regional and national levels and finally compete for major scholarship awards. This program is co-sponsored by leading industries as well; and it serves North and South Dakota students as well as those from Minnesota schools.

The State Science Fair and Research Paper Program climaxes the selection process for choosing Minnesota's participants in the Junior Symposium described above. Also an annual event, the State Sc ience Fair is presented in alternate years at a Twin Cities location (The Minneapolis Lemington hotel in recent years) or at another Minnesota city, usually a college town.