APPARENT COMPETITION AND THE DIFFERING EFFECTS OF GENERALIST AND SPECIALIST PREDATORS ON CERVID POPULATIONS

by

Hannah Silvaggio

An Undergraduate Thesis Submitted in Partial Fulfilment of the Requirements for the Degree of Honours Bachelor of Environmental Management

Faculty of Natural Resources Management

Lakehead University

May 2020

Dr. Brian McLaren	Dr. Bill Severud
Thesis Supervisor	Second Reader

LIBRARY RIGHTS STATEMENT

In presenting this thesis in partial fulfilment of the requirements for the H. B. E. M. degree at Lakehead University in Thunder Bay, I agree that the University will make it freely available for inspection.

This these is made available by my authority solely for the purpose of private study and research and may not be copied or reproduced in whole or in part (except as permitted by the Copyright Laws) without my written authority.

Signature: _____

Date: __2020/04/23__

A CAUTION TO THE READER

This H. B. E. M. thesis has been through a semi-formal process of review and comment by at least two faculty members. It is made available for loan by the Faculty of Natural Resources Management for the purpose of advancing practice of professional and scientific forestry.

The reader should be aware that opinions and conclusions expressed in this document are those of the student and do not necessarily reflect the opinions of either the thesis supervisor, the faculty or Lakehead University.

ABSTRACT

Silvaggio, H. L. 2020. Apparent competition and the differing effects of generalist and specialist predators on cervid populations.

Apparent competition is an important ecological function that has been extensively studied in wild cervid populations, but little is known about how to manage it or why some cervid populations are more affected by it than others. This meta-analysis attempts to give insight about how much numerical response to increases in competing alternate prey occurs for a generalist (*Canis lupus*) or specialist (*Puma concolor*) predator. The rate of change (λ) and survival rate of cervid prey populations affected by apparent competition were extracted from multiple studies and it was found that there was little to no difference in either parameter for the populations hunted by the two different predators. This suggests that more factors, like the habitat in the areas inhabited by multiple predators, need to be researched to obtain a clear understanding of the theory involving apparent competition.

Keywords: Apparent competition hypothesis, predator-prey interactions, specialist/generalist predators.

ACKNOWLEDGEMENTS

Thank you to my mother who listened to my ramblings about wildlife all these years and supported and encouraged me to the end with my decision to pursue a career in wildlife conservation. Thank you to Dr. Brian McLaren for agreeing to be my supervisor and guiding me in the right direction each time I decided on a different topic to pursue. And thank you to Dr. Bill Severud for agreeing to be the second reader of this thesis and for your recommendations on this final draft.

CONTENTS

INTRODUCTION

It has been shown many times over in ecology that creatures in a forested environment hang within a very delicate balance of each other. One of the ways we attempt to describe changes to this balance is by focusing on predator-prey interactions, particularly on how their relationship with each other influences their respective population densities. More specifically, we have descriptions of how the introduction of a new, abundant prey species (primary prey) within an area is followed by higher predation of native prey species (secondary prey) due to rising predator densities. The effect is known as *apparent competition* (Holt 1974) and it has proven to be quite challenging to manage (DeCesare et al. 2010). This ecological interaction may not be entirely determined by the opportunistic apex predators that take advantage of the abundant prey, but hyperpredation does amplify the effects of apparent competition.

A common solution in wildlife management is to enact a cull for the predator, but it is often short-lived. Because the abundant prey remains available, the original predator population will re-establish its numbers or a new predator will take advantage of the cull and move into the newly unoccupied area (Serrouya et al. 2011). This method of predator management is very controversial in contemporary times and often results in public outcry for the persecuted predators. A recent example of alternative methods in action is the management of the declining caribou (*Rangifer tarandus*) on Michipicoten Island near Wawa, Ontario in 2018. The caribou decline was elicited by a pack of advantageous wolves (*Canis lupus*) that were being sustained by both the caribou during the winter and an enormous population of beavers (*Castor canadensis*) in the summer

(Patterson et al. 2017). The public wished for the wolves to be spared culling and the result of this situation included translocation of the remaining caribou, the death of almost the entire wolf pack due to starvation, and a less than favourable public perception on current wildlife management (Fletcher 2018). Could there have been a better outcome of this situation had the attention been on reducing the primary prey (beavers) of the wolves on the island rather than the caribou?

To answer this kind of question, this thesis will be focusing on the resulting changes to vital statistics in the prey due to the numerical response of predators to prey species in apparent competition. A numerical response is reflected in the change of the number of predators within a region due to the prey abundance changing (Mills 2013). The resulting numerical response of a predator can help us have a deeper understanding of the current state of both predator and prey populations, as well as aid predicting their futures. I will be analyzing how this response differs between generalist and specialist predators by performing a meta-analysis of other management situations, similar to Michipicoten Island, where a cervid population is experiencing decline due to excessive predation prompted by apparent competition.

The two predators of focus are the gray wolf, representing a generalist predator, and the cougar or mountain lion (*Puma concolor*), representing a specialist predator. These two predators were chosen because they are two iconic Canadian predators and they represent most of the current available research regarding apparent competition in Canada. Deer population density is estimated to respond more to predation by generalist predators rather than to predation by predators with specialized prey preferences. It is expected that wolves, as social carnivores, will have more successful hunts than

cougars, which are solitary hunters (Feldhamer et al. 2015). Wolves exhibit cooperative parental care, which leads to greater fecundity and contributes to exponential growth, whereas in cougars, only single mothers take care of their offspring and do not have the advantage of a pack to support them (Ausband 2019; Feldhamer et al. 2015; Hornocker and Negri 2009). These differences should be reflected by a lower population growth and survival rate in deer populations that are primarily preyed upon by wolves.

LITERATURE REVIEW

Effects of predation on cervid population trends

An inspiration for this study is one of the works of Stan Boutin that critiqued the methodology of previous studies focusing on moose population dynamics and predation (Boutin 1992). Boutin emphasized that it is important to determine whether predation of moose by wolves is a limiting factor (implying a moose population reduction) or a regulating factor (where equilibrium is achieved in the moose population after the perturbance). He performed a meta-analysis on previous studies and found multiple discrepancies in them regarding their methodology and results. Two issues that were focused on were the effects of other predators not being taken into account and the varying reports on losses of moose due to hunting by humans. Only one of the studies addressed whether predation on moose population was density dependent. All studies calculated the total number of moose killed based on wolf scat analysis in the summer and observation of kills in winter, not taking into account different biases for each of these approaches.

Another early publication that is influential to this study was by Francois Messier, who conducted a similar meta-analysis to what Boutin achieved (Messier 1994). In this case, the main objective was to determine if wolf predation alone can regulate moose populations based on the data from numerous studies. Messier concluded that the relationship between moose density and wolf predation is different when moose density is at the lower end of its range in a manner of relaxation of the functional and numerical response of the wolves. However, he acknowledged error with this conclusion because certain factors, such as alternate prey species present, body size

variation of wolves in different areas, and differences in methodology, confounded the meta-analysis. My approach focused on some of the issues brought up by these two authors.

Causes of apparent competition and decline in wild cervid populations

While the concept of apparent competition may be plainly stated, pinpointing specific causes for it may not be so clear. The rapid increase in population size of a primary prey species can be accredited to many factors. A common factor among many studies that focus on apparent competition is the fragmentation and destruction of wildlife habitats caused by humans (DeCesare et al. 2010). For example, all of the studies on declining woodland caribou (currently listed as endangered by the Committee of Endangered Wildlife in Canada, COSEWIC, in 2012) list human habitat alteration as the main driving force for apparent competition (Hervieux et al. 2014; Johnson et al. 2019; Kinley and Apps 2001; Serrouya et al. 2015, 2017, 2019; Wittmer et al. 2007). Human-altered habitat often elicits introduction of non-native prey species or the alteration of prey assemblages (DeCesare et al. 2010). Secondary prey is often less fecund and/or more vulnerable to increased predation than the introduced prey, which is the case for woodland caribou and why apparent competition can eventually lead to extirpation of secondary prey (Serrouya et al. 2015). Although the results of apparent competition can be quite devastating to the affected secondary prey, its implications and management methods for cervid species were limited until recent years when the quick decline of woodland caribou populations garnered public and media attention.

METHODOLOGY

This research was accomplished as a meta-analysis. There was a focus on articles from the Canadian and northern United States region to keep the forest types relatively consistent. This study will not be limited to one prey species, but rather expand to include other species of cervids that both generalist and specialist predators are known to prey on: moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*),mule deer (*O. hemionus*), elk (*Cervus canadensis*) and woodland caribou.

Keywords were searched in the Web of Science to include apparent competition, prey switching, alternate prey, secondary prey and hyperpredation to find relevant research. The next step, because of its contribution to the study of apparent competition and inspiration for this thesis, a subset of studies was chosen if the authors cited DeCesare et al.'s article *Endangered apparently: The role of apparent competition in endangered species conservation*, or the works of Robert Serrouya or Stan Boutin. Additional papers by the same author using the same data were excluded, as were papers on human hunted populations. Using these exclusion criteria, I was able to decrease the initial results of the search in Web of Science, 107 articles, to 16 articles to read. Out of these, 11 were considered for this analysis, until I decided to exclude the Kinley and Apps (2001) data because the small sample size of cougars was acknowledged to have biased the analysis (see Appendix), This decision left 10 articles for the final analysis. The articles were summarized in two tables: 1) Apparent competition with *Canis lupus* as the generalist predator, and 2) Apparent competition with *Puma concolor* as the specialist predator.

It was reported that no additional predators occurred in either system. Values for survival rate extracted from the articles were limited to adult females, as all the studies used were concerned with the population and survivability of mature, reproducing females. To determine the overall effect that each predator type had on each deer species, averages across the two tables for rate of population change, lambda (λ), and for survival of adult females were compared.

RESULTS

The most common primary prey that initiated apparent competition is the white-tailed deer, which was the case for 7 of the 10 studies analyzed (Tables 1 & 2). Moose follow closely behind, appearing in 6 of the 10 studies as primary prey; elk appeared in 2 studies, and mule deer in 1 study. The woodland caribou is the most common secondary prey.

Despite their vast differences in hunting behaviour, the average rate of change (λ) of deer populations hunted by wolves or cougars was very similar. Arithmetic mean for population growth rates in deer hunted by a generalist predator was $\lambda=0.93$, and for specialist predators $\lambda=0.91$, respectively. The average female survival rate was 0.85 (generalist) and 0.84 (specialist). These results suggest that the numerical response of wolves or cougars as a shared predator in an apparent competition scenario is neither much higher or lower than the other.

Table 1. Apparent competition with *Canis lupus* as the generalist predator.

Secondary prey	Primary prey	Location	λ [1]	Female survival [1]	References
Woodland caribou	Moose	Prince George, BC	~ [2]	0.84	Wittmer et al. 2007
Woodland caribou	Moose	Columbia & Cariboo Mtn, BC	~	0.86	Serrouya et al. 2017
Woodland caribou	Moose, elk, white-tailed deer	West-Central AB	0.99	0.91	Hervieux et al. 2014
			0.86	0.79	
Woodland caribou	Moose	BC and Quebec	0.94	~	Johnson et al. 2019
			0.99	~	
Elk	Moose, elk, white-tailed deer	BC and AB	~	0.83	Hebblewhite et al. 2018
Woodland caribou	Moose, white-tailed deer, mule deer	BC, AB, and Idaho, USA	0.93	~	Serrouya et al. 2019
			0.95	~	
			0.86	~	
			0.98	~	
			0.86	~	
			0.87	~	
			0.91	~	
			0.97	~	
			0.95	~	
			0.90	~	
			0.95	~	
			1.00	~	
			0.93	~	
			0.91	~	
			0.92	~	
			0.73	~	
			1.09	~	
	Mean:		0.93	0.85	

[1] λ and female survival refer to the secondary prey.
[2] ~ refers to data unavailable within the study.

Table 2. Apparent competition with *Puma concolor* as the specialist predator.

Secondary prey	Primary prey	Location	λ [1]	Female survival [1]	References
Mule deer	White-tailed deer	South-central BC	0.88	0.72	Robinson et al. 2002
Woodland caribou	White-tailed deer	~	0.90	~	Serrouya et al. 2015
Mule deer	White-tailed deer	Selkirk Mountains, BC	0.84	~	Wielgus 2017
Elk	White-tailed deer	South Dakota, USA	1.03	0.95	Lehman et al. 2018
		Mean:	0.91	0.84	

[1] λ and female survival refer to the secondary prey.
[2] ~ refers to data unavailable within the study.

DISCUSSION

Contrary to the original hypothesis for this analysis, deer populations hunted by wolves and cougars displayed similar values despite the two predators' vast differences in hunting method and social behaviour. While the dataset for cougar hunted populations is notably smaller than wolf hunted populations, their similarities may not be so surprising after all. Despite their elusive nature, cougars have still proven themselves to be a formidable and influential apex predator. Wolves typically prefer older and/or weaker prey (Mech and Nelson 2013), cougars have been observed to have a profound effect on deer populations. Pumas, on the other hand, are more likely to take healthy, breeding adults out of a population because of their 'opportunistic prey

preferences,' meaning they will take advantage of easy prey if it is available to them (Horne et al. 2019). In past studies not included in this analysis, cougars have exhibited a higher proportion of elk kills than wolf packs inhabiting the same area (83 *versus* 53 for calves, 42 *versus* 39 for adult females; Elbroch et al. 2013). Male cougars are also more likely than female cougars to take a chance at killing a moose or elk with calf at heel, so a cougar population with a greater ratio of males to females may cause a dramatic decline in deer populations suffering from apparent competition.

A common issue with studies of predator-prey interactions, including the studies in this analysis, is that only one predator's response to one prey is recorded and the authors take no account of how the presence of other predators and prey affect the responses they observe (Chan et. al 2017; Boutin 1992). It is likely that there were other predators affecting the population dynamics of the secondary species in the studies I cite, but only one predator was considered in each study. For example, American black bears (*Ursus americanus*) are known to take deer neonates, and during the summer season black bears can consume more prey than wolves do (Merkle et al. 2017). The presence of additional predators is just one of many factors that must be analyzed in order to properly grasp and manage such a complex ecological interaction as apparent competition.

CONCLUSION

This analysis, while it does provide insight into the effect that a shared generalist or specialist predator may have on a deer population, is by no means conclusive on the subject of apparent competition. More concrete results may have been achieved if more data could have been found in studies with cougars as the specialist shared predator.

This may be personal error, or the research may not be available at this point in time. In future studies that wish to pursue this specific or similar topics, I would suggest trying to use different search methods to find more applicable studies or maybe broaden the region for the search.

LITERATURE CITED

Ausband, D. E. 2019. Pair bonds, reproductive success, and rise of alternate mating strategies in social carnivore. Behavioural Ecology 30(6): 1618-1623.

Boutin, S. 1992. Predation and moose population dynamics: A critique. Journal of Wildlife Management 56(1): 116-127.

Chan, K., S. Boutin, T. Hossie, C. J. Krebs, M. O'Donoghue, and D. L. Murray. 2017. Improving the assessment of predator functional responses by considering alternate prey and predator interactions. Ecology 98(7): 1787-1796.

DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: The role of apparent competition in endangered species conservation. Animal Conservation 13: 353-362.

Fletcher, R. 2018. So, what becomes of the wolves? Sault Star. www.saultstar.com /news/local-news/so-what-becomes-of-the-wolves. Sept 26, 2019.

Feldhamer, G. A., L. C. Drickamer, S. H. Vessey, J. F. Merritt, and C. Krajewski. 2015. Mammology: Adaptation, Diversity, Ecology (4th Edition). Johns Hopkins University Press. Pages 491-493.

Hebblewhite, M., D. R. Eacker, S. Eggeman, H. Bohm, and E. H. Merrill. 2018. Density-independent predation affects migrants and residents equally in a declining partially migratory elk population. Oikos 127: 1304-1318.

Hervieux, D., M. Hebblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. Canadian Journal of Zoology 92(12): 1029-1037.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. American Naturalist 12: 197-229.

Horne, J. S., M. Hurley, C. White, and J. Rachael. 2019. Effects of wolf pack size and winter conditions on elk mortality. Journal of Wildlife Management. 83(5): 1103-1116.

Hornocker, M., and S. Negri. 2009. Cougar: Ecology and Conservation. University of Chicago Press. Pages 61-65.

Johnson, C. J., M. A. Mumma, and M. H. St.-Laurent. 2019. Modeling multispecies predator prey dynamics: predicting the outcomes of conservation actions for woodland caribou. Ecosphere 10(3): 1-23.

Kinley T. A., and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin 29(1): 158-164.

Kunkel, K., & D. Pletscher. 1999. Species-specific population dynamics of cervids in a multipredator ecosystem. Journal of Wildlife Management. 63(4): 1082-1093

Kunkel, K., T. Ruth, D. Pletscher, and M. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park Montana. Journal of Wildlife Management 63(3): 901-912.

Lehman, C. P., C. T. Rota, J. D. Raithel, and J. J. Millspaugh. 2018. Pumas affect elk dynamics in absence of other large carnivores. Journal of Wildlife Management 82(2): 344-353.

Mech, L. D., and M. E. Nelson. 2013. Age structure of moose (*Alces alces*) killed by gray wolves (*Canis lupus*) in northeastern Minnesota, 1967–2011. Canadian Field-Naturalist 127: 70-71.

Merkle, J., J. Polfus, J. Derbridge, and K. Heinemeyer. 2017. Dietary niche partitioning among black bears, grizzly bears, and wolves in a multiprey ecosystem. Canadian Journal of Zoology 95: 663-671.

Messier, F. 1994. Ungulate population models with predation: A case study with North American moose. Ecology 75(2): 478-485.

Mills, L. S. 2013. Conservation of Wildlife Populations: Demography, Genetics, and Management (2nd Edition). John Wiley and Sons Ltd. Pages 142-152.

Patterson, B., J. Benson, K. Middel, K. Mills, A. Silver, and M. Obbard. 2013. Moose calf mortality in Central Ontario, Canada. Journal of Wildlife Management 77(4): 832-841.

Patterson, B., A. Rodgers, J. Shuter, C. Dersch, S. Kingston, and E. McCaul. 2017. Wolf recolonization threatens caribou persistence on Michipicoten Island, Ontario. Conservation and Ecology of Mammals – Carnivores. web.archive.org/ web/20170905050646 /http://twsconference .org/sessions/ conservation-and-ecology-of-mammals-carnivores. Sept 26, 2019.

Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. Canadian Journal of Zoology 80: 556-568.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015. Using predator-prey theory to predict outcomes of broadscale experiments to reduce apparent competition. American Naturalist 185(5): 665-679.

Serrouya, R., B. N. McLellan, H. van Oort, G. Mowat, and S. Boutin. 2017. Experimental moose reduction lowers wolf density and stops decline of endangered caribou. PeerJ 5:e3736.

Serrouya, R., D. R. Seip, D. Hervieux, B. N. McLellan, R. S. McNay, R. Steenweg, D. C. Heard, M. Hebblewhite, M. Gillingham, and S. Boutin. 2019. Saving endangered species using adaptive management. Proceedings of the National Academy of Sciences 116(13): 6181-6186.

Wielgus, R. B. 2017. Resource competition and apparent competition in declining mule deer (*Odocoileus hemionus*). Canadian Journal of Zoology 95(7): 499-504.

Wittmer, H. U., B. N. McLellan, R. Serrouya, and C. D. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. Journal of Animal Ecology 76: 568-579.

APPENDIX

Apparent competition with a wolf as generalist predator					
Secondary prey	Primary prey	lambda (pop growth)	survival rates	References	
woodland caribou	moose		0.84	Wittmer et al. (2007)	
woodland caribou	moose		0.86	Serrouya et al. (2017)	
woodland caribou	moose, elk, white-	0.99	0.91	*Hervieux et. al (2014)	Studied different subpops in AB
woodland caribou	moose, elk, white-	0.86	0.79	*Hervieux et. al (2014)	
woodland caribou	moose	0.94		Johnson et al. (2019)	Subpops in BC & QC
woodland caribou	moose	0.99		Johnson et al. (2019)	
elk	moose, white-tailed		0.83	Hebblewhite et al.	
woodland caribou	, white-tailed deer, mu	0.93		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.95		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.86		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.98		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.86		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.87		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.91		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.97		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.95		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.9		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.95		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.9		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	1		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.93		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.91		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.92		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	0.73		Serrouya et al. (2019)	
woodland caribou	, white-tailed deer, mu	1.09		Serrouya et al. (2019)	
		0.93	0.846		

Apparent competition with cougar as specialist predator				
Secondary prey	Primary prey	lambda (pop growth)	survival rates	References
mule deer	white-tailed deer	0.88	0.72	Robinson et al. 2002
woodland caribou	white-tailed deer	0.9		Serrouya et al. (2015)
mule deer	white-tailed deer	0.84		Wielgus (2017)
elk	white-tailed deer	1.03	0.95	Lehman etal (2018)
		0.9125	0.835	
woodland caribou	moose, elk, deer	0.62		Kinley & Apps (2001)