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Winter population dynamics between the Eastern Wolf (*Canis lycaon*) and the Common Raven (*Corvus corax*) in Algonquin Park, Ontario

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Abstract
The eastern wolf (*Canis lycaon*) is important to the Algonquin Provincial Park ecosystem through its top-down influences on the food web. While previous research in Yellowstone National Park has shown that the common raven (*Corvus corax*) is dependent upon wolves to survive winter, this relationship has never been fully explored in Ontario. This study examines the patterns of abundance between wolves and ravens in the Algonquin Park area between 1988 and 1998 using data from an 11-year wolf population study and raven counts from the Christmas Bird Count database. Due to their common winter feeding strategy, I predicted that raven numbers would rise and fall during similar years as wolf populations. While raven numbers were affected by wolf population size, abundances were negatively correlated. I propose that this relationship is explained by wolf pack size; as pack size increases wolves can more adequately defend against raven scavengers and consume the carcass more effectively therefore neutralizing the raven's strategy of group foraging. Future study should aim to address these trends at a longer and more recent time scale. This investigation highlights the advantages and limitations of using citizen science to compliment scientific research.

Keywords
Ecology — Historical populations — Species interactions — Scavenging — Wolves — Ravens

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1. Introduction

To survive, an animal must eat and avoid being eaten. However, successful foraging becomes increasingly difficult in patchy landscapes when food supplies are concentrated in few locations across large distances. In these landscapes, many scavengers are forced to capitalize on brief opportunities to feed on fresh animal carcasses. Such is the case for species like the common raven (*Corvus corax*, henceforth raven), whose challenge to forage successfully becomes increasingly difficult come winter when alternative food supplies are limited. Fortunately, ravens are opportunistic scavengers (Heinrich, 1988) and a generalist species that can take advantage of the sudden pulses in food supply (Wilmers et al. 2003). The strategy of social foraging is also important as sharing information allows them to sample across greater distances and increases their chances of finding food (Bugnyar and Kostrschal, 2001; Szipl et al. 2015). Additionally, recruitment of larger flocks neutralizes attacks from territorial adult ravens (Marzlufi et al. 1991) and increases the scrounging success from a kill defended by predators (Henrich, 1988). The term scrounging refers to the ability of an individual to exploit food made available by others, and this strategy is commonly employed by ravens at wolf carcasses (Bugnyar and Kotrschal, 2002). The advantages of social foraging have been shown to increase with the scarcity and patchiness of food supplies (Clark and Mangel, 1984).

Ravens have learned to use wolf packs to find and access fresh kills as it offers them a reliable food source throughout winter (Harrington, 1978). Wolves are reported to lose large amounts of food to scavengers, such as ravens (Smith et al. 2003; Stahler et al. 2006). Raven searching strategies include listening for wolf communication through howls, following them directly to a fresh kill or flying overhead while wolves pursue prey (Harrington, 1978; Stahler et al. 2002). Although ravens commonly take on a "thieving" role, they have sometimes been known to lead wolves to a dying or recently dead ungulate which is advantageous as ravens cannot break through thick hides on their own (Heinrich, 1988).

The eastern wolf (*Canis lycaon*) is important to the Algonquin Park ecosystem through its top-down influence on the food web (J.B. Theberge and M.T. Theberge, 2004). Wolves maintain a balance in prey populations through predation on sick and weak animals as well as healthy ones (OMNR, 2007). Additionally, they stimulate the reproduction of prey populations and provide food for scavengers (OMNR, 2007). While previous research has shown that ravens are dependent upon this predator to survive winter (Vucetich et al. 2004), this relationship's effect on population abundances over time has never been fully explored in Ontario.

In the past, research has been handicapped by short term

funding or inadequate sampling periods. This study combines data from an 11-year Algonquin Park wolf population study (J.B. Theberge and M.T. Theberge, 2004) and raven abundances from the Christmas Bird Count's database (henceforth CBC). I tested the hypotheses that the number of ravens counted in winter throughout the Algonquin Park area would be affected by wolves due to their shared winter feeding strategies. I predicted that as the Algonquin Park wolf population increased, the raven numbers in the area would also increase, and vice versa, as an increase in the number of wolves would result in more kills and therefore more food for ravens.

2. Methods

2.1 Study Area

Data from Algonquin Provincial Park was used as it provided a long enough time scale to examine raven-wolf abundance due to its valuable implications for conservation and the availability of scientific research. This park is located between Georgian Bay and the Ottawa River in Central Ontario, Canada and lies in the transition area between Ontario's northern coniferous forests and the province's southern deciduous forests.

2.2 Data Collection

Wolf population numbers between 1988 and 1998 were obtained from the J.B. Theberge and M.T. Theberge's study (2004) and raven numbers were obtained from the Christmas Bird Count (CBC) online database for the same years. The research by J.B. Theberge and M.T. Theberge (2004) was the longest intensive wolf study ever conducted in Canada and was designed to understand the role of wolves in Algonquin Provincial Park's ecosystem (7,653km^2) and surrounding area. Furthermore, their study hoped to determine essential information about long-term wolf population dynamics. Wolf data collection was conducted using three sampling techniques; aerial surveys, radio-telemetry and snow tracking.

Raven numbers were summed across seven (24km diameter) count circles in the Algonquin Park area to provide a similar temporal and spatial comparison between the two species (Figure 1). Each 458km^2 area was surveyed once every winter, and counts were made between 14 December and 5 January in order keep the sampling period consistent and avoid time of year bias. Winter data was used as this is when ravens are most dependant on wolf kills and when there is less influence from alternative food sources.

The six additional CBC circles surrounding Algonquin Park were: North Bay, Burk's Falls, Gravenhurst/Bracebridge, Minden, Pembroke and Deep River (Figure 1). These were included in the analysis as 1) they increased the raven sampling area from 458km^2 to 3206km^2 which allowed raven results to be more comparable to the area used by wolves (Algonquin Park (7,653km^2)) and 2) these additional plots accounted for the fact that ravens and wolves are not restricted by park boundaries. The Algonquin wolf study recorded the wolves' migration outside of the park particularly in the winter when they were forced to travel further following prey populations (J.B. Theberge and M.T. Theberge, 2004). Additional literature emphasizes the dispersal tendencies of wolves in Ontario (OMNR, 2005).

2.3 Data Analyses

The number of ravens and wolves were plotted in order to observe trends between years. A linear regression was used to describe the yearly trends in raven and wolf numbers. A correlation analysis was used to determine the strength and direction of the wolf-raven relationship. Additionally, a second correlation analysis was conducted using the number of ravens "per party hour" to take into account observer effort. Birds-per-party hour was calculated as the total number of birds seen divided by the number of total party hours spent in the field counting those birds.

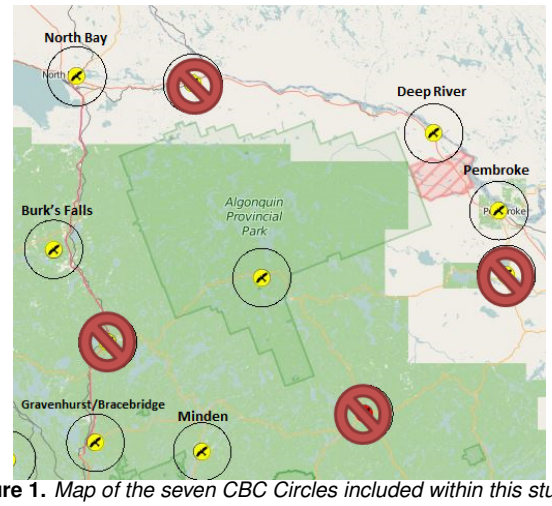

Figure 1. *Map of the seven CBC Circles included within this study (map taken from the CBC website). Circles crossed out were not included in analysis due to insufficient data. Total park area is 7,653 km^2 and individual count circles are 458 km^2.*

3. Results

During the sample period (1988-1998), peak raven numbers tended to correspond with declines in the wolf population and vice versa (Figure 2). Ravens rose on average 53 birds per year while wolves declined approximately three wolves per year throughout the 11-year study.

A significant negative correlation was found between wolf and raven abundances (Figure 3; $R = -0.62$, $F_{1,10} = 5.73$, $p = 0.04$). Thirty-nine-percent of the variation in raven numbers could be explained by wolf population size (Figure 3).

A similar correlation was found after considering observer effort (Figure 4; $R = -0.61, F_{1,10} = 5.92, p = 0.038$). Wolf abundance explained 40% of the variation in raven abundance between years (Figure 4).

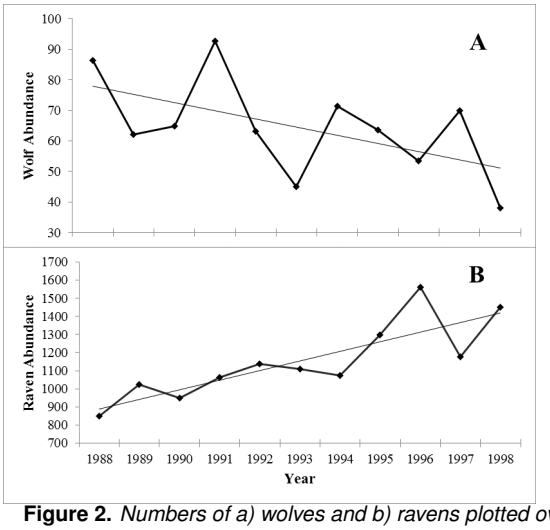

Figure 2. *Numbers of a) wolves and b) ravens plotted over time.*

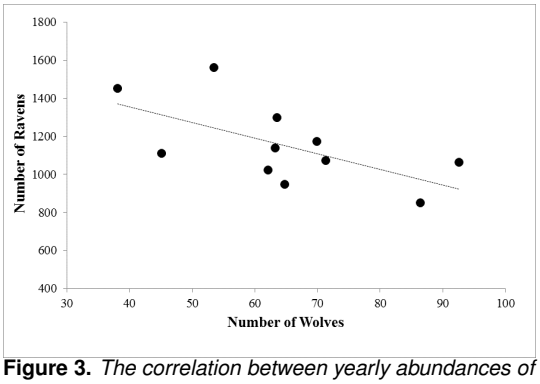

Figure 3. *The correlation between yearly abundances of wolves and raven.*

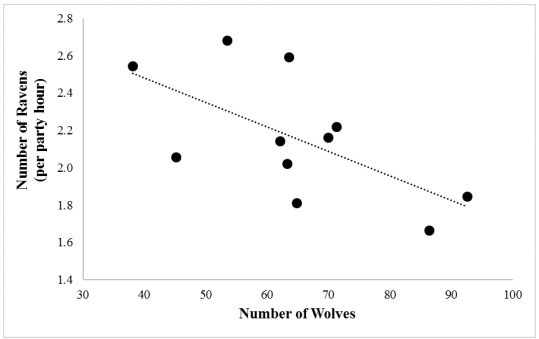

Figure 4. *The correlation between yearly abundances of wolves and ravens (per party hour).*

4. Discussion

Lower number of wolves led to higher numbers of ravens. This could be explained by feeding strategies used by these two species. Wolves are adapted to a "feast-or-famine" lifestyle where at times they go weeks without food before making a kill, and therefore must consume as much meat as possible when they do (Stahler et al. 2006). They have been known to eat up to 10 kg of meat during the initial round of feeding and once full, they must rest in close proximity to the carcass before feeding again (Stahler et al. 2006). This break is the ravens' opportunity to get a meal, however frequency of these occasions depend on both the size of the kill and the wolf pack (Vucetich et al. 2004).

Larger wolf packs can more adequately defend against scavengers and more efficiently consume an entire carcass without pause (Schmidt and Mech, 1997). This suggests that while kills could be more numerous in years with larger wolf packs, less of that food would be accessible to the ravens. The social foraging of ravens becomes particularly advantageous in years with smaller wolf packs as it increases each ravens chance of scrounging food (Hayes et al. 2000; Vucetich et al. 2004), especially as kills become scarcer and further distributed across the landscape (Clark and Mangel, 1984). Rather than literal increases in raven numbers, more individuals may have been observed throughout the eleven years of CBC data as they flocked together more often for foraging trips as wolf numbers declined.

Unfortunately, raw data for wolf pack size throughout this study period were not available; however in the Algonquin wolf study the mean pack size variation was graphed over time (J.B. Theberge and M.T. Theberge, 2004, see Appendix A). This shows that wolf pack size increased and decreased accordingly with wolf population size. This factor could offer explanation for the variation in raven numbers which was not a result of wolf population changes (Figure 2a). Further study is required to examine not only the relationship between raven numbers and pack size but also other factors affecting raven abundances, such as corvid body condition, food caches and intraspecific interactions. While not all factors affecting raven-wolf interactions have been examined here, it is valuable to acknowledge a biological linkage between the two species seen within the Algonquin Park area.

Wolf declines throughout the study period were mainly attributed to hunting, since both weather and prey populations did not vary significantly over the 11-year study (J.B. Theberge and M.T. Theberge, 2004). While wolf hunting was prohibited within the park's boundaries, it was not banned outside its perimeter. The research showed that as whole packs were killed, the other wolf pack territories increased to fill the gaps (J.B. Theberge and M.T. Theberge, 2004). Therefore, anthropogenic impacts on wolf numbers could have implications on other species, such as the ravens. According to J.B. Theberge and M.T. Theberge (2004) approximately two-thirds of all Algonquin Park wolf mortality was human-caused, espe-

cially in the townships south of the park. Fifty-eight percent of wolves killed by humans died in two deer yards outside the park. These facts emphasize once again the importance of considering influences outside of park boundaries. The wolf population decline seen throughout the 11-year study (Figure 2a) was reportedly maintained only by immigration. This shows that wolf packs outside of the park influenced the wolf numbers recorded in this study and this further supports the inclusion of the seven CBC raven sampling circles within the Algonquin Park area.

While CBC data provide reliable historical documentation of avian populations, interpretation is still accompanied by unavoidable bias as experience of the observers can influence numbers and species recorded. For example, ravens could have been mistaken for american crows (Corvus brachyrhynchos) however, CBC protocol protects against this by assigning a competent and experienced observer to each sampling area to confirm identification.

A potential source of error from count sampling could be over-estimation due to repeated sightings of the same individual. If kills become more scarce or distributed further across the landscape as wolf numbers decline then ravens must increase their search effort (Heinrich and Marzluff, 1991) this in turn could increase the number of ravens being counted. Additionally, if raven abundances are not distributed evenly across the landscape, places of raven concentration or absence could also influence estimations of raven abundance.

Anthropogenic food sources, such as city dumps, may be subsidizing raven diet throughout the winter. The placement of CBC count circles tended to be focused on human settled areas, which is a disadvantage, as abundance numbers may not be representative of the surrounding habitat in which the wolves live.

Future studies should confirm whether the observed pattern is consistent in recent years as human pressures and environmental conditions continue to change. Research should also aim to improve the quality of raven sampling and further explore the use of citizen science to compliment scientific studies.

In conclusion, wolf numbers seem to influence raven winter abundances over time in Algonquin Park. This can in part be explained by wolf pack size and the foraging techniques of these two species although future studies should examine other factors influencing this relationship.

Acknowledgments

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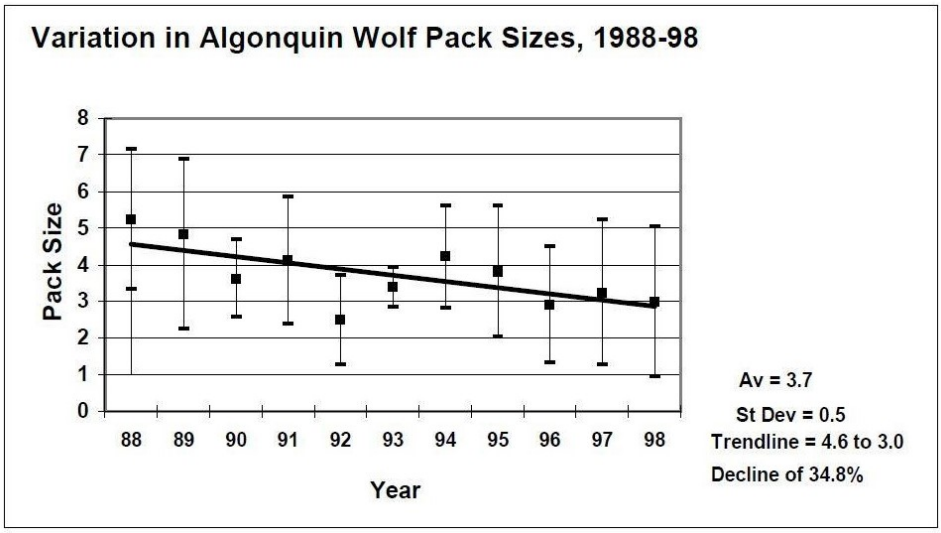
Appendix



Appendix A. *Changes in wolf pack size from 1988 to 1998 as reported in the Algonquin wolf study (J.B. Theberge and M.T. Theberge, 2004).*

Appendix B. *Raw data listing yearly Algonquin Park wolf numbers and total raven numbers between all seven CBC circles.*

Time (years)	Number of Wolves	Number of Ravens	Number of Ravens/Party hour
1988	86.4	850	1.6667
1989	62.1	1023	2.1424
1990	64.8	948	1.8116
1991	92.6	1063	1.8474
1992	63.2	1138	2.0213
1993	45.1	1110	2.0582
1994	71.3	1073	2.2211
1995	63.5	1299	2.5913
1996	53.5	1561	2.6807
1997	69.9	1175	2.1635
1998	38.1	1451	2.5443