

ESTIMATES OF ABUNDANCE AND PREDATION - THE POPULATION
ECOLOGY OF BEAVER IN ISLE ROYALE NATIONAL PARK

by

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This thesis, "Estimates of abundance and predation - the population ecology of beaver in Isle Royale National Park," is hereby approved in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE IN APPLIED ECOLOGY.

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PREFACE

The population dynamics of the beaver (*Castor sp.*) are fairly well studied and beaver are predominantly thought to have a strong top-down influence on the ecosystems they inhabit (*see review in* Rosell et al. 2005). Despite widespread acceptance of beaver as a keystone species and ecosystem engineer, the impacts of predation on the population dynamics of beaver are almost completely ignored (*for exception see* Potvin et al. 1992). Myself and the co-authors identified here have taken advantage of long-term data available for both beaver colony and wolf abundance on Isle Royale National Park to initiate assessments on the top-down influences of predation, bottom-up impacts of forest succession and the importance of abiotic processes as factors contributing to beaver population dynamics.

Beaver colonies are typically surveyed in the fall of the year, when their food cache is visible. Normally aircraft are used to accomplish this work. As part of ensuring an accurate count, investigators often employ a “double-count” survey. This survey involves two independent observers, each recording observations. These observations are then compared to one another and an estimate for the entire population is obtained, including those members of the population of interest not seen by either observer. We have completed 5 double-count surveys on Isle Royale between 1990 and 2008 to increase the accuracy of our abundance estimate for beaver colonies. In two of those surveys, 1990 and 2002, a large fixed wing aircraft housing pilot and both observers was used. Specifically, this aircraft was a DeHavilland Beaver. In the remaining counts,

2006-2008, we used two smaller fixed-wing aircraft (Aeronca Champ or Aviat Husky) each with its own pilot and observers. Unexpectedly, sightability, probability of detecting a beaver colony, was lower from the smaller aircraft, whose flight speed was slower, altitude lower and flight pattern was circling as opposed to the high altitude and straight flight line of the larger aircraft. Surprisingly, overestimation of sightability in the larger aircraft only became apparent after use of the smaller aircraft. Our results are important for others who employ the double-count method, in so much as, application of the double-count method can give scientists false confidence in meeting the assumptions associated with the double-count method.

Predation plays a crucial role in the biodiversity and function of ecosystems (Duffy 2002, Duffy et al. 2007). Generally, this importance is quantified in terms of mean abundance of consumers and resources available to these consumers. Less frequently investigated are the varying time scales at which consumer (predator) and resource (prey) abundances interact with each other. We manipulate the spatial-temporal aspects of the wolf, moose and beaver colony data collected on Isle Royale between 1962 and 2009, as well as, aspects of forest succession in each of three distinct forested communities to articulate the meaningful time scales at which top-down, bottom-up and abiotic processes influence beaver population dynamics. This approach is interesting for three reasons; (i) it incorporates the role of predation in beaver population dynamics which has largely been ignored previously, (ii) it allows us to quantify the influence of predation on the population of not only beaver, but also in a novel way, assess the impacts of beaver as a bottom-up influence on wolf population dynamics, and (iii)

contemplate restoration of beaver populations, both in North America and Europe, where in much of the beaver's former range restoration occurred in the absence of predation. Without elucidating what role predation plays in beaver population dynamics we may be operating under misconceptions regarding exactly what ecosystem processes we have restored.

The story of beaver and beaver research in Isle Royale National Park began in 1790 and does not end here, but rather will continue because dedicated people care and this story is worth telling. I have attempted to provide a brief synopsis of this story to date in Appendix A. This snapshot is intended to give context to our efforts here and hopefully give the reader perspective regarding beaver ecology and its heretofore largely overlooked role in a unique ecosystem whose wolf-moose / predator-prey interactions have drawn attention away from this “ecosystem engineer”. The work in Chapters 1 & 2 of my thesis, although I hesitate to say “my”, is largely our efforts to compile and extract a small aspect of the work done by Phillip Shelton, Rolf Peterson, and Doug Smith. These individuals kept the interest in beaver ecology on Isle Royale alive despite already demanding workloads. With the help of John Vucetich, who clarified our thoughts and provided important insights, I hope we have initiated a good start to what undoubtedly requires more concentrated effort to address key aspects of beaver ecology that perhaps can be more fully exacted on Isle Royale than anywhere else.

CHAPTER 1: Double-count surveys and unexpectedly misleading estimates of sightability for beaver colonies.¹

Abstract

An important method for estimating the abundance of wildlife is the double-count method, which involves comparing numbers of organisms seen by two independent observers. We used the double-count method to estimate sightability and number of North American beaver (*Castor canadensis*) colonies in Isle Royale National Park (Lake Superior, North America). In 1990 and 2002, we used the method with two observers flying in a DeHavilland Beaver. In 2006, 2007, and 2008, we used two observers in separate, smaller aircraft that flew transects and circles at lower altitudes. Unexpectedly, sightability was lower from the smaller aircraft. Specifically, sightability had been 0.84 (95% CI = [0.78, 0.90]) for the smaller aircraft and 0.96 (95% CI = [0.92, 0.99]) for larger aircraft. However, other evidence suggests sightability had been grossly overestimated for the larger aircraft. Sightability when flying higher and straighter, required in the larger aircraft, may have been ~0.50. Overestimation arose from violating an assumption of the double-count method – the assumption that all lodges are equally sightable. Disturbingly, that violation became apparent only after surveys from the smaller aircraft. The results are an object lesson where, the double-count method gave reason to think observers had a high rate of detecting colonies, when in fact it had been much lower.

¹ We submitted a manuscript based on this chapter for peer-review with authorship as follows: Romanski, M.C., J.A. Vucetich, D.W. Smith, R.O. Peterson, and P.C.Shelton; this manuscript is currently in review.

INTRODUCTION

The effects of North American beaver are profoundly important for many boreal forests at a variety of spatial scales from the watersheds of small drainages to the landscape level (Collen and Gibson 2001, Müller-Schwarze and Sun 2003, Rosell et al. 2005). At the landscape level, the influences of beavers are greatly impacted by their population dynamics. Although long-term studies that document population dynamics of beaver are rare, the few that exist suggest beaver populations fluctuate substantially from year to year (Hood and Bayley 2008). Long-term studies also suggest the longevity of individual colonies varies greatly among colonies even when total abundance is relatively stable (Fryxell 2001).

Because beavers are important and because their populations are so dynamic, it is important to understand the accuracy of various methods for estimating beaver abundance. In principle, the size of a beaver population is the number of active colonies in an area multiplied by the average colony size. In many cases, it is possible or considered adequate to know about temporal fluctuations in number of colonies, without knowing much about fluctuations in colony size (Hood and Bayley 2008). An important method for estimating colony abundance is aerial survey (Hay 1958, Payne 1981, Smith and Peterson 1991, King et al. 1998, Hood and Bayley 2008).

More generally, the double-count method is valuable for more accurately assessing abundance and sightability for a wide variety of wildlife species (e.g., Estes and

Jameson 1988; Anthony et al. 1999; Smith et al. 2004; Fletcher and Hutto 2006; *see also* Skalski et al. 2005). From an estimate of sightability, one can estimate the number of animals or objects that existed but went undetected. The essence of double-counting is for two observers to record their observations independently, and then compile a list of individuals that were detected only by observer A, only by observer B, and by both observers A and B. From these lists, one can estimate the number that neither detected and a total population size.

In this paper, we report the results of double-count surveys conducted from two different kinds of aircraft. The results are important because they show how a double-count method can, under certain circumstances, give a misleading impression for the sightability of objects surveyed from aircraft.

STUDY SYSTEM

Isle Royale is a forest-covered island (544 km²) located in the northwest portion of Lake Superior, North America (48°N, 89°W). The island is approximately 71 km long, 7.7 km wide, and characterized by a series of ridges and valleys that run parallel to Isle Royale's long axis.

Many of the island's valleys are occupied by habitat suitable for beavers (Linn 1957). The island's ridge-valley topography is most pronounced at the northeast portion of the island, where glaciers left little soil and much exposed bedrock, and less

pronounced at the southwest portion of Isle Royale where glaciers deposited more soil (Huber 1973). Consequently, the northeast portion of Isle Royale contains more lakes and streams. Overall, 7.2% of the island's area is characterized as lakes, ponds, wet meadows, or marshes, and the island includes approximately 254 kilometers of stream.

Except for a few bays, the Lake Superior shoreline is exposed to wave and ice action that is often extreme, and is characterized by cold, oligotrophic waters that support very little aquatic vegetation. From extensive boat and canoe travel conducted by the authors during each of the past 40 years, it is known that beaver lodges are rarely constructed on the Lake Superior shore line of Isle Royale except in protected embayments.

Most of Isle Royale's forests are dominated by boreal species (white spruce [*Picea glauca*], balsam fir [*Abies balsamea*], aspen [*Populus tremuloides*], and cedar [*Thuja occidentalis*]) and some stands contain important components of northern hardwood species (sugar maple [*Acer saccharum*] and yellow birch [*Betula alleghaniensis*]).

Beavers were likely extirpated from Isle Royale during the 19th century, and recolonized the island early in the 20th century (Shelton 1966). Isle Royale's current beaver population has not been harvested or otherwise managed for approximately 100 years. Their population dynamics are thought to be influenced both by forest succession and predation by wolves (*Canis lupus*, see Chapter 2), which have also not been harvested. Moreover, beaver are likely influenced by the indirect effects of a high-

density moose (*Alces alces*) population which affects both wolf abundance and forest dynamics (Vucetich and Peterson 2004a, b).

FIELD METHODS & DATA PREPARATION

Aerial Survey

To estimate abundance of active beaver colonies and temporal trends in colony abundance, aerial surveys were conducted in 19 of the 46 years between 1962 and 2008. All surveys were conducted in October after leaves had fallen from deciduous trees and before snow covered the ground or ice covered the lakes. Ranging from 3.5 to 17 hours, the average survey was 10.2 hours (± 47 min. SE; $n = 20$) of flying conducted within a period spanning three to five days.

The surveys involved flying NW-SE transects across the west end of Isle Royale, where beaver habitat is relatively rare. At the east end of Isle Royale where beaver habitat is more common, the plane flew along all of the drainages (which run NE-SW). The plane circled back when the observer felt the need for a longer view to detect and record a colony. Finally, because colony density was especially high in the small area at Isle Royale's northeast end, that region was flown twice.

A colony was judged active on the basis of various sign, typically a lodge and food cache. Other signs taken to represent an active colony included: freshly peeled sticks, newly cut trees or shrubs, canals, fresh mud on a lodge, recently repaired dam, or

sometimes a cache without a lodge (Hay 1958; Payne 1981; Brown & Parsons 1982; Swenson et al. 1983).

Between 1962 and 2004, the observers for all surveys were PCS or DWS who flew in one of several different kinds of aircraft. In most years the aircraft was a two-person (observer and pilot), tandem-seat aircraft (i.e., Piper PA-18, Piper J-3, Aviat Husky, or Aeronca Champ). However in 1988, 1990, 1998 and 2002, surveys were flown in a DeHavilland Beaver, which is a larger aircraft. All aircraft were fixed-wing, high-wing and single engine.

In 1990 and 2002, surveys also involved the double-count method, with PCS and DWS flying together in a DeHavilland Beaver. One observer sat in the front right seat and the second observer seated behind the first. Each observer recorded locations of colonies independently. These double-count surveys were intended to estimate the sightability of beaver colonies and the proportion of colonies in the population that tend to go undetected. This double-count procedure was conducted in 1990 for a portion of the island that contained 134 active colonies that had been detected by at least one observer, and in 2002 for a portion that contained 60 active colonies that had been detected by at least one observer.

In 2006, 2007, and 2008, the double-count method was employed in a different manner. For each of these years, colonies were counted independently by two different observers (ROP and MCR), each flying in different aircraft. Each aircraft was a two-person, tandem-seat plane (i.e., Aviat Husky or Aeronca Champ). For each of these

surveys, the two observers flew over the same portions of the island within two days of each other.

In 2008, the survey included 35 sites seen by both observers, but judged differently by the observers as to whether the site represented an active or inactive colony. To address these differences, we developed more rigorous criteria for *post hoc* classification. Specifically, a colony was considered active if at least one observer recorded the presence of: (i) a cache that included more than just a few sticks, (ii) a lodge or dam with fresh mud and freshly cut trees or shrubs nearby, or (iii) canals with freshly cut trees or shrubs nearby. A site was not considered an active colony unless it had a cache, even if that site included a lodge or dam with fresh mud. In previous surveys, fresh mud or caches with only a few sticks had been considered, by themselves, to be adequate evidence of activity. The observers took sufficient notes during the survey flights to apply these newer criteria to the 2008 survey.

Analysis

We estimated sightability for each of the 5 double-count surveys, and compared sightability estimates derived from the different types of aircraft. From these estimates of sightability, we also estimated total abundance of active colonies for all 19 surveys, including the 15 that did not include a double count. Finally, we compared estimates of abundance based on the two sets of criteria used in 2008 to judge whether a site represented an active or inactive colony.

Sightability.– The formulas we used to estimate sightability and abundance are taken from Skalski et al. (2005:452). Specifically, the probability that observer A will detect a lodge is $P_A = N_{AB}/(N_B + N_{AB})$ where N_{AB} is the number of lodges that both observers A and B had detected and N_B is the number of lodges detected only by observer B. The probability that observer B will detect a lodge is $P_B = N_{AB}/(N_A + N_{AB})$ where N_A is the number of lodges detected only by observer A. The adjusted Lincoln-Peterson estimate for lodge abundance is

$$N_{total} = ((N_A + N_{AB} + 1)(N_B + N_{AB} + 1) / (N_{AB} + 1)) - 1. \quad \text{Eq. 1}$$

The estimated probability that an active lodge will be detected by at least one observer is $P_d = 1 - (1 - P_A)(1 - P_B)$. The 95% confidence interval for abundance is

$N_{total} \pm z_{0.025} \sqrt{Var[N]}$, where

$$Var[N_{total}] = \frac{(N_A + N_{AB} + 1)(N_B + N_{AB} + 1)(N_A)(N_B)}{(N_A + 1)(N_B + 1)(N_{AB} + 2)} \quad \text{Eq. 2}$$

We calculated 95% confidence intervals for P_d as

$$\left[\frac{(N_A + N_{AB}) + (N_B + N_{AB}) - N_{AB}}{(N_{total} - z_{0.025} \sqrt{Var[N_{total}]})}, \frac{(N_A + N_{AB}) + (N_B + N_{AB}) - N_{AB}}{(N_{total} + z_{0.025} \sqrt{Var[N_{total}]})} \right].$$

The formal assumptions associated with these equations include (Skalski et al. 2005): (1) the population being closed to immigration and emigration during each survey, (2) the detection of a colony by one observer has no effect on the probability that the other observer will detect it, (3) all colonies are correctly identified as having been

sighted by just one observer or by both observers, and (4) all colonies have an equal probability of being detected.

Abundance. – For the three double-count surveys conducted after 2004, abundance was calculated according to Equation (1). For the 15 single-count surveys conducted between 1962 and 2004, we estimated total abundance as the total number of detected colonies (N_d) divided by the mean probability of detection for each single observer (e.g., For PCS, $P_{ave} = (P_{1990} + P_{2002}) / 2 = (0.78 + 0.79) / 2 = 0.785$, see results and Table 1).

The single-count survey of 2004 was an exception. Specifically, logistical constraints and poor weather prevented flying over the southwestern portion of Isle Royale and caused the densely populated, northeast portion of Isle Royale to be flown over once, rather than twice (*see Methods*). In past surveys, this southwestern portion of Isle Royale has contained, on average, 15% of the population's colonies. Also, in previous surveys, when the densely populated region had been flown over a second time, the result was, on average, the detection of 29% additional colonies for that region. The 2004 survey detected just 40 colonies, including 8 colonies in the densely populated region. We adjusted N_{total} by first adding the number of colonies that were likely to have been detected had a second fly-over been conducted (i.e., by adding $10.3 = 8 \times [1 + 0.29]$), and then by dividing that quantity by $(1 - 0.15)$ to account for the colonies that would have likely been detected in the southwest region of Isle Royale.

To estimate total abundance for the double-count survey conducted in 1990, we accounted for the fact that the survey did not cover the southwest portion of Isle Royale. Again, we adjusted N_{total} by dividing it by $(1 - 0.15)$.

The double-count survey conducted in 2002 also did not cover the southwest portion of Isle Royale, but did include a single count for that region. Here we estimated N_{total} as $60/P_d + 13/P_{ave}$, where 60 is the number of colonies detected by at least one observer for the double-count portion of the survey and 13 is the number detected by the single observer who flew the single-count portion of the survey.

RESULTS

Compared to estimates based on smaller aircraft, the estimated sightability was greater when based on observations from the larger aircraft, the DeHavilland Beaver (Table 1-1; Fig. 1-1). Specifically, the overall probability of detection (P_d) was 0.96 (95% CI = [0.92, 0.99]) for the larger aircraft and 0.84 (95% CI = [0.78, 0.90]) for the smaller aircraft.

The point estimate in 2008 for sightability was also greater when criteria for judging the activeness of a colony were more rigorous compared to the sightability estimate associated with the less rigorous criteria (Table 1-1). Specifically, estimated sightability was 0.88 (95% CI = [0.80, 0.97]) when criteria for colony activity was more rigorous and 0.85 (95% CI = [0.76, 0.95]) for the same survey observations and less

rigorous criteria for colony activity. While the difference in sightability is not statistically significant, the difference in estimated abundance is more important ($P < 0.05$). Specifically, the more rigorous criteria led to an estimate of 128 colonies (95% CI = [107, 150] and the less rigorous criteria led to an estimate that was 17% greater (i.e., 150 colonies (95% CI = [127, 173])).

Survey results associated with the double-count method suggest that active beaver colonies increased, on average, 0.49 yr^{-1} for each of the two years between 2004 and 2006. Only under very rare circumstances can a mammal the size of a beaver exhibit such high growth rates (Okie and Brown 2009). Because the 2004 survey involved some extrapolation and did not employ the double-count method, it is also useful to consider that active colonies increased, on average, 0.15 yr^{-1} for each of the four years between 2002 and 2006. The appearance of dramatic increase is also indicated inasmuch as the number of colonies detected by any single observer in 2006 and afterward was, in most cases, greater than for the 2004 or 2002 surveys, even though estimated sightability for any single observer had been much lower in 2006 and afterward (Table 1-1).

DISCUSSION

Colony abundance appears to have increased between 2004 and 2006 to levels that had not been estimated since 1996 (Fig. 1-2). Despite the appearance of dramatic increase, other evidence suggests colony abundance should have declined or remained stable, especially throughout the period 2002-2008. That period was characterized by severe,

multiyear drought with each of the six years experiencing below average summer precipitation (Western Regional Climate Center 2009). The second driest summer in the past 70 years occurred in 2007. The drought was also associated with what appears to be long-term shifts in habitat. Several drainages that were occupied by beavers prior to the mid-1990s had become sedge meadows by 2008. The meadows became dry enough to support a breeding population of sand hill cranes (*Grus canadensis*) for the first time during the study period. The 2006 survey was also associated with the disappearance of several beaver colonies that had been present for several previous surveys.

Overestimation

Several considerations suggest the discrepancy between expected decline (or stability) and apparent increase in colony abundance is explained by misleading estimates of sightability that resulted in gross underestimates of lodge abundance during the 1990s and early 2000s.

First, the 2006-2008 surveys were associated with styles of flying that differed from prior surveys. In earlier surveys, the plane flew at approximately 240-300 m above the ground and only occasionally circled back to take longer views for detecting colonies. From 2006 onward, the plane flew approximately 90-150 m above the ground and flew overlapping circles over all stream and drainage habitat. The tendency for circling to result in greater sightability has been reported elsewhere for surveys of other kinds of wildlife (Evans et al. 1966, Peterson & Page 1993).

Moreover, the 1990 and 2002 double count was conducted in a DeHavilland Beaver, whereas the 2006-2008 double counts were conducted in smaller, tandem-seat aircraft. The smaller aircraft tend to fly slower (95-130 km/hr compared to 175-200 km/hr) and the windows of the smaller aircraft allow for a substantially better view of the ground.

To better understand how earlier double counts overestimated sightability and to appreciate the potential generality of the problem, consider an extreme case. Suppose that a population is comprised of two types of colonies and that each type is equally abundant. One type is almost always seen by any observer from a DeHavilland Beaver flying high and straight, and a second type that is virtually impossible for any observer to detect under those flying conditions. The apparent sightability would be nearly 100%, but the actual sightability would be ~50%. This circumstance represents a violation of an assumption for the double-count method, specifically, the assumption that all lodges have an equal probability of detection. Importantly, that violation became apparent only after conducting a double-count survey with different aircraft and flying style.

From a smaller plane with better visibility that flew lower and circled more, a pair of observers would see a greater proportion of the difficult-to-detect colonies. The result would be detection of more colonies, but a lower estimate of sightability. This is the pattern that was observed (Table 1-1). In the future it may be possible to further improve estimates of sightability by observing and then modeling the factors that affect a

colonies' sightability (e.g., Fletcher and Hutto 2006). Factors affecting sightability might include cache size or whether a lodge is on a stream or lake.

Other factors

Differences in sightability were associated not only with different types of aircraft and styles of flying, but also different observers. Prior to 2006, double-count surveys were conducted by PCS and (or) DWS. From 2006 onward, surveys were conducted by MCR and ROP. Because ROP and DWS each have several thousand hours of experience counting wildlife from aircraft, it seems unlikely that differences in observer skill explain much, if any, of the discrepancies. Moreover, PCS (who conducted most of the surveys) appears to have a similar ability to detect colony as DWS (Table 1-1).

Colony sightability may also have declined at some point in (or throughout) the period, 1962-2008. In the 1960s average colony size had been estimated as 6.4 beavers (Shelton 1966). Today, colony size is likely smaller, and smaller colonies may construct smaller caches and lodges that are more difficult to detect (Easter-Pilcher 1990). Nevertheless, the proportion of colonies without caches have remained stable for the period from 1962-2008 (0.157 ± 0.015 [Mean $\pm$ SE]; $P < 0.001$, single sample t -test, $n = 19$). Ultimately, it seems difficult to judge whether colony size had changed enough between 2002 and 2006 to result in important changes in sightability.

Reconciliation

Because colony surveys had been conducted to better understand temporal trends in beaver population dynamics, it may be appropriate to adjust upward the estimates of abundance for surveys when sightability had been overestimated. To better understand the degree of overestimation, ROP observed colonies in October 2008 from a two-person, tandem-seat aircraft flying over a portion of Isle Royale using two different flying styles. With the improved flying style (frequent circling at lower altitudes) he detected 42 active colonies, with the poorer flying style (straight transects at higher altitudes) he detected 28 of those colonies and two colonies that had not been detected by the improved flying style. These values suggest sightability is 0.67 (95% CI = [0.52, 0.81]) for the poorer flying style and 0.93 (95% CI = [0.84, 1.00]) for the improved style. However, if one considers that ROP's overall sightability for 2008 had been 0.75, and if the 42 colonies detected by the improved style represents only 75% of the colonies that actually existed, then the best point estimate for the sightability while flying transects at higher altitude may be ~ 0.50 ($=0.75 \times 0.67$).

If sightability had been 0.50, then estimates of colony abundance for surveys with the poorer flying style should be equal to twice the number of colonies detected. If these circumstances are applied to survey results from the late 1990s and early 2000s, one would have the impression that lodge abundance had, in general, been declining during the past decade.

It remains unclear whether the sightability of earlier surveys (1962-2004) had always been low, or whether sightability had been deteriorating over a period of time. Consequently, it also remains unclear whether all earlier surveys should be treated as though sightability had been 0.50. Unfortunately, we may never gain a better sense about this issue.

Implications

Double-count surveys are an important technique for estimating the abundance of wildlife populations. Surveys resulting in estimates of high sightability give confidence about the accuracy and precision of the survey. We experienced such circumstances, and were surprised when subsequent double-count surveys, conducted with a different type of aircraft and flying style showed how the earlier estimates of sightability had been grossly overestimated.

One is reminded of when Justice Oliver Wendell Holmes, Supreme Court Associate Justice 1902-1932, said, “Certitude is not the test of certainty.” Our findings seem like an object lesson for many applications of the double-count method, aside from those associated with beaver colonies, certain aircraft, or flying techniques. It may not always be obvious when the assumption of equal sightability is being violated with as much consequence as we had experienced.

Much wildlife research is based on observations made from the DeHavilland Beaver and similarly large aircraft flying transects at elevations of 240-300 m above the ground. However, smaller, slower, lower-flying aircraft may generally result in substantially better observations.

Our findings also highlight a special challenge for long-term monitoring and research. This time series of colony abundances represents one of the longest in existence (*see also* Hood and Bayley 2008). Long-term research can either tend towards methodological consistency over time, or tend to adopt methods thought to represent improvements. Effective incorporation of improved methods is critically valuable, but requires human and financial resources that allow substantial periods where both new and old methods can be conducted at the same time.

ACKNOWLEDGEMENTS

This research was made possible with financial support from the Isle Royale & Keweenaw Parks Association, the National Park Service's Great Lakes Inventory and Monitoring Program, Isle Royale National Park and a grant to ROP and JAV from the National Science Foundation (DEB-09182497). The work was also made possible by several pilots from the National Park Service, Superior National Forest and Up North Aerials.

Table 1-1. Statistics associated with the double count method for aerial surveys of active beaver colonies conducted in Isle Royale between 1990 and 2008.

	N_A	N_B	N_{AB}	P_A	P_B	P_d	N
1990	112	110	88	0.8	0.79	0.96	164*
2000 [†]	73	—	—	—	—	0.8	91
2002	50	49	39	0.8	0.78	0.96	79*
2004 [†]	50	—	—	—	—	0.8	59
2006	92	58	41	0.69	0.44	0.83	133 [117, 149]
2007	84	43	29	0.67	0.35	0.79	124 [103, 144]
2008	97	65	49	0.75	0.51	0.88	128 [107, 150]
2008 [‡]	102	70	49	0.7	0.47	0.85	150 [127, 173]
2008 [§]	42	30	28	0.93	0.67	—	—
prior to 2006	162	159	127	0.8	0.78	0.96	—
2006 -2008 [¶]	273	166	118	0.71	0.43	0.84	—

Symbols: N_A and N_B are the total number active colonies detected by observers A and B, respectively. N_{AB} is the number of active colonies detected by both observers A and B. P_A and P_B is the probability of detection for observers A and B, respectively. P_d is the probability an active colony would be detected by at least one of the two observers. N is the adjusted Lincoln-Peterson estimate of total abundance. Values in brackets are 95% confidence intervals.

Notes:

(*) Estimated abundance is calculated according to text described in *Abundance*.

(†) Double counts surveys were not conducted in 2000 or 2004, these years are included for the purpose of comparing numbers of colonies detected by single observers between 2000 and 2008. The values of P_d for these rows are the value of P_d that was calculated for observer A for the time period “prior to 2006.” Confidence intervals are not presented for these cells because data necessary to do so does not exist (see Equation 2).

(‡) Values in this row represent statistics when more permissive criteria were used as evidence to judge whether a colony was active (See *Methods* for details.).

(§) In this row N_A represents colonies detected over a portion of Isle Royale when the flight pattern involved circling at low altitude and N_B represents colonies detected over the same area when flying transects at higher altitude.

(||) Values for N_A , N_B and N_{AB} for this row are the sum of the same values reported for 1990 and 2002.

(¶) Values for N_A , N_B and N_{AB} for this row are the sum of the same values reported for 2006, 2007, and 2008.

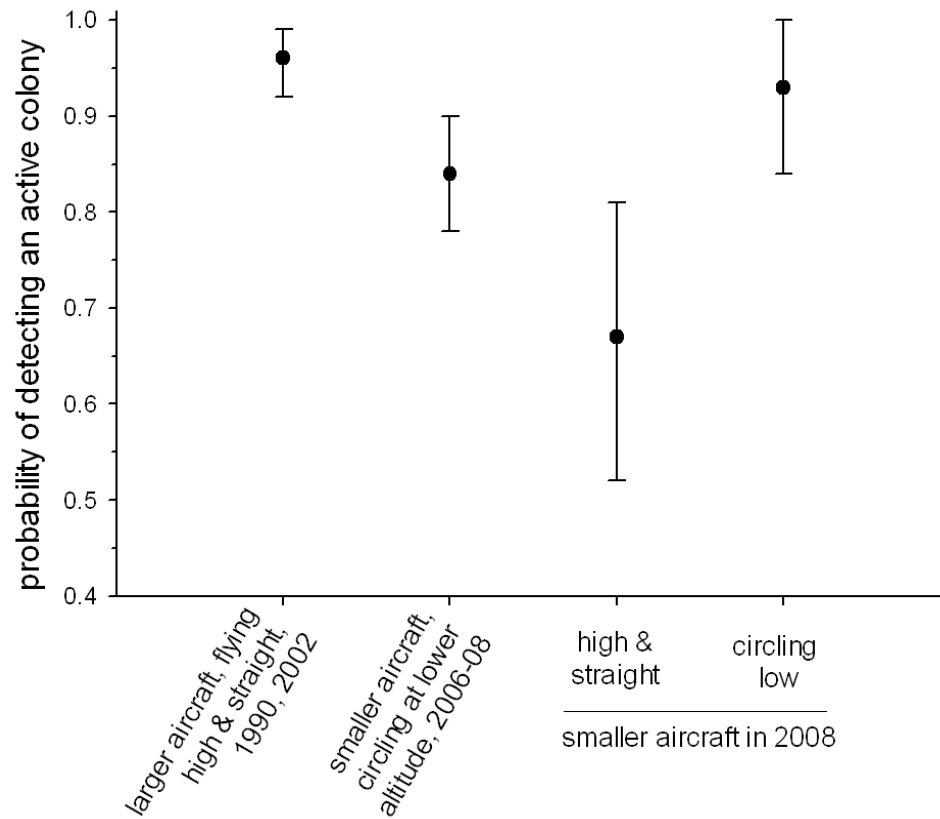


Fig. 1-1. Estimated probabilities of detecting an active beaver colony under various conditions. The first two points are estimated probabilities that at least one of two observers will detect an active colony. The last two points are estimated probabilities that an observer will detect an active colony from a smaller aircraft under two different flying conditions. The difference between the first and third points indicates the extent to which the first point overestimates the probability of detection. Aircraft types are described in the *Methods*, and flying styles are further described in the *Discussion*. Vertical bars are 95% confidence intervals.

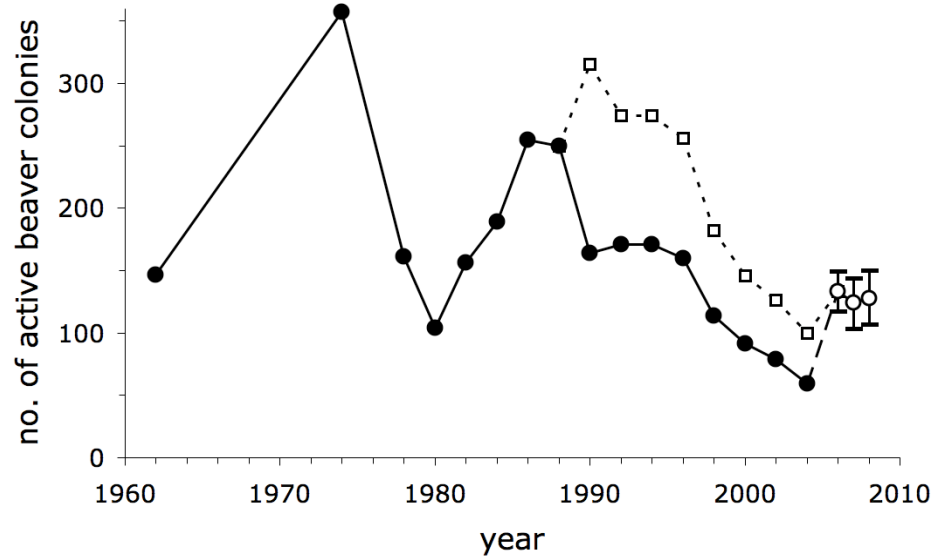


Fig. 1-2. Estimated abundances of active beaver colonies on Isle Royale, 1962-2008. Most values (●) are the number of colonies detected divided by the sightability (96%) estimated from double-count surveys conducted in 1990 and 2002. Recent estimates (○) were based on sightabilities estimated from double-count surveys conducted in each of those years from smaller aircraft that flew circles over beaver habitat at lower altitudes (see Table 1). Open squares (□) represent estimates of abundance that account for the extent to which sightability may have been overestimated (see *Reconciliation*). Vertical bars (2006-2008) are 95% confidence intervals (see Table 1-1).

CHAPTER 2: The fourth dimension's influence on top-down, bottom-up and abiotic regulation of beaver population dynamics.²

ABSTRACT

Predation, a top-down process, is often implicated as a strong control in ecosystem function and trophic cascades. Conversely, the influences of forest succession, or more generally, “bottom-up” processes, are thought to be the primary regulatory agent in beaver (*Castor sp.*) population dynamics. We took advantage of spatial-temporal variability in North American beaver (*Castor canadensis*) colony abundance on Isle Royale National Park (Lake Superior, North America) to explore the influences of top-down, bottom-up and biotic processes on the population ecology of beaver. Beaver colony abundance for each of three, distinct, forested regions on Isle Royale is well correlated. However, the forest succession trajectories in these regions are not synchronized. Consequently, on Isle Royale, beaver population dynamics are not entirely explained by forest succession. We conducted aerial surveys to estimate active beaver colony abundance, and census the wolf (*Canis lupis*) and moose (*Alces alces*) populations from 1962-2009. Additionally, we used occurrence of beaver in wolf feces as a surrogate for predator diet to estimate annual predation rates, the proportion of the annual beaver population consumed by wolves. Beaver colony abundance importantly explained the proportion of wolf diet that was beaver, which averaged ~14% for the period. Mean predation rate was ~0.16 and was significantly explained by wolf

² We will submit a manuscript based on this chapter for peer-review with authorship as follows: Romanski, M.C., J.A. Vucetich, R.O. Peterson, P.S. Shelton, and D.W. Smith; target date for submission is June 2010.

abundance. Climate data, mean annual precipitation and mean annual stream flow as surrogates for water availability representing abiotic processes, did not influence beaver population dynamics for the period. Interestingly, beaver population dynamics were an important, albeit short-lived, bottom-up influence for wolf population dynamics. Interactions between wolves and its focal prey, moose, and alternate prey, beaver, may represent apparent competition that could have long-term, negative impacts for beaver population dynamics. In a larger context, beaver populations are importantly influenced both from the top-down and the bottom-up and these influences can be more aptly interpreted when applied to an appropriate temporal scale.

INTRODUCTION

A central theme in ecology is to understand the influence of predation on ecological communities. In this context, much research has focused on trophic cascades which involves assessing whether the presence of a predator has a positive, indirect effect on vegetation, by reducing the abundance of an herbivore population (*see review in* Schmitz et al. 2000, Terborgh et al. 2001, Douglas et al. 2008, Ripple and Beschta 2009). It is much less common to investigate the influence of predation by focusing on a herbivore population and assessing the relative extent to which its population dynamics are influenced by bottom-up processes (resource availability), top-down processes (predation), and abiotic processes (e.g., climate). Research in population dynamics often

distinguishes between processes that occur on slower or faster time scales (Levin 1992, e.g., Krebs et al. 2001). However, assessments of predation's influence on community dynamics rarely distinguishes between influences occurring on slower time scales (e.g., long-term average or trends in abundance) and those occurring on faster time scales (e.g., inter-annual variability around a long-term trend in abundance). In many instances, trophic cascade research examines how a predator affects mean abundance (Cardinale et al. 2006). Here we investigate the potential influence of top-down, bottom-up, and abiotic processes on the population dynamics of beaver (*Castor canadensis*). In doing so, we distinguish between processes that might operate on slower and faster time scales.

Wolf-ungulate-vegetation systems have become very well studied with respect to understanding the influence of predation on terrestrial communities (e.g., McClaren and Peterson 1994, , Berger et al. 2001, Vucetich and Peterson 2004a, Hebblewhite et al. 2005, Ripple and Beschta 2007, Beyers et al. 2007, Bump et al. 2009). For many landscapes, the influence of wolf predation on beaver populations and their ecological effects could be as important as wolf-ungulate-vegetation relationships. Despite its potential importance, this set of relationships has gone almost completely unstudied. One reason for neglect is that long-term data useful for elucidating beaver population dynamics coupled with wolf population dynamics is rare. Here we investigate the dynamics of a beaver population that was surveyed during 21 of the 47 years between 1962 and 2009.

It is widely appreciated that beavers have a strong top-down influence, manifest over relatively long time scales, on the composition of forest communities (Naiman et al. 1986, Donkor and Fryxell 1999, Barnes and Mallik 2001, Cunningham et al. 2006). Beavers alter forest composition by preferentially foraging on deciduous trees and tending to avoid coniferous trees. These shifts in forest composition are associated with shifts in ecosystem functioning, such as nutrient cycling (Naiman and Melillo 1984, Naiman et al. 1994). Beavers also have important impacts on the aquatic systems they inhabit, affecting vegetation, fishes communities, stream morphology, and nutrient dynamics (Johnston and Naiman 1987, Johnston and Naiman 1990a-c, France 1997, Gurnell 1998, Collen and Gibson 2001). Beaver herbivory can also lead to the declines in resource abundance for beavers, which in turn can lead to their decline at local site (Johnston and Naiman 1990, Moen et al 1990, Pastor and Naiman 1992, Fryxell 2001). Conventionally, forest fires are thought to be critical for restoring the resource abundance that beavers may have previously depleted (Barnes and Mallik 2001; *for exception see* Hood and Bayley 2007). Though most beaver research has focused on these processes, which occur at relatively slower rates, inter-annual variability in resource availability also seems to be an important aspect of beaver population dynamics (Fryxell 2001, Campbell et al 2005; Hyvonen and Nummi 2008). These observations justify the conventional impression that beavers are important ecosystem engineers because of their strong top-down influences (Jones et al. 1994). However, this perspective may be incomplete for neglecting the potential influence that wolf predation may have on beaver population dynamics.

Understanding the role of wolf predation on beaver-dominated communities would be interesting for two general reasons. First, although wolves commonly prey on beavers, beavers are not wolves' primary prey (Mech 1966, Voigt et al. 1976, Fuller 1989, Peterson 1977, Thurber and Peterson 1993, Forbes and Theberge 1996, Urton and Hobson 2008). This observation suggests the plausible, but untested, hypothesis that while wolves may have a strong top-down influence on beavers, beavers are less likely to have a strong bottom-up influence on wolves. Predation on beavers would be subsidized by wolves' predation on ungulates. Nevertheless, it is also plausible that, in some years or during certain seasons, beavers are important for wolf survival or reproductive success. In this way, there is potential for wolf-beaver interactions to be mediated by apparent competition with moose, wolves' focal prey on Isle Royale.

The second reason for interest in wolf predation in beaver-dominated communities is that one of the great conservation successes in the 20th century is the restoration of beavers to many of the landscapes where they had previously been extirpated (Müller-Schwarze and Sun 2003; Rosell et al. 2005). The superficial presumption is that beaver restoration is associated with the restoration of the community and ecosystem processes with which beavers had been involved (e.g., Albert and Trimble 2000). However, wolf predation has not been restored to many of the landscapes where beavers have been restored. If wolf predation is an important component of beaver-dominated communities, then the restoration of beavers, in many places, has not been associated with the restoration of wolves' influences. Outside of Isle Royale, these

landscapes are dominated by processes that would have been uncharacteristic of those operating prior to extirpation of wolf-beaver interactions (e.g., Bridgham et al 1995).

Here, we investigate the dynamics of a beaver population that has been monitored over a five decade period (1962-2009) on Isle Royale National Park, an island in Lake Superior, North America. This population has been exposed to significant temporal variation in wolf predation and climatic conditions. This beaver population is also characterized by Isle Royale's landscape which includes three regions, each a discrete forest community that has been following its own distinct succession trajectory. We exploited this spatial-temporal variability to assess how this beaver population may have been affected by top-down, bottom-up, and abiotic processes.

Study System

Isle Royale National Park is a forest-covered island (544 km²) located in the northwest portion of Lake Superior, North America (48°N, 89°W). Isle Royale is a long (~70 km), narrow (~7.8 km) island characterized by three distinct regions, an eastern region dominated by boreal forests, a western region dominated by northern hardwood forests, and a central region characterized by a severe forest fire that occurred in 1936 (Fig. 2-1). The dominate tree species in the eastern region are white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and mountain ash (*Sorbus Americana*; Linn 1957). This region is also

characterized by a high density of streams and lakes that lie in a series of parallel valleys that were created by the retreat of the Wisconsin glacier 9400 years before the present (Huber 1973). The western region is dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula allaghaniensis*), and cedar (*Thuja occidentalis*) and characterized by fewer inland lakes and streams. The central region is dominated by paper birch, aspen, white pine (*Pinus strobus*) and jack pine (*Pinus banksiana*) and intermediate density of inland lakes and streams. The boundaries of these regions are defined by their fire histories. The central region is defined by and characterized by a severe, stand-replacing forest fire that occurred in 1936 (Linn 1957). Charcoal analysis of sediment cores extracted from three inland lakes indicate fire has occurred infrequently in the western region over the past 300 years, however, the eastern two-thirds of Isle Royale experienced a fire interval of approximately every 100 years dating back to the 1500s (Flakne and Cole 1995). This disturbance was largely attributed to human activities (i.e., trapping, logging and mining). Since establishment as a National Park in 1931, these forests have experienced little to no large-scale disturbance, the 1936 fires excluded (National Park Service 2004).

Beaver were likely extirpated on Isle Royale during the late 19th century, but recolonized the island by the early 20th century. For this study, the average number of beaver colonies for the period was 131 (SE = 13, interquartile range [79, 204]) and ranged from 50 to 286 colonies. Between 1961 and 1963, Shelton (1966) determined a mean colony size of 6.4 beavers for Isle Royale. Elsewhere, colony size ranges from 4.1 to 8.2 beavers per colony (Müller-Schwarze and Sun 2003). Density, number of beaver colonies per km of stream for the study period, is comparable to that of other populations

(0.52 ± 0.05 [mean $\pm$ SE]; Hartman 1997). Isle Royale is also inhabited by a wolf population that first arrived in about 1950. Approximately 90% of the wolves' diet is moose, and the remainder is beaver (Thurber and Peterson 1993). Wolves are the only predators of moose and beaver on Isle Royale. The density of wolves has been high compared to many other wolf populations (interquartile range: [18, 27] wolves and [33, 50] wolves/1000 km²). Moose have been present on Isle Royale since the beginning of the 20th century. Their densities are also comparatively high (interquartile range: [650, 1100] moose and [1.2, 2.1] moose/km²). The wolf-moose-forest interactions are known to be strong and complex (Vucetich and Peterson 2004 a, b). Coyotes (*Canis latrans*) and white-tailed deer (*Odocoileus virginianus*) are absent from the island, and muskrats (*Ondatra zibethicus*) are rare. None of these populations has been hunted or trapped by humans for nearly a century.

FIELD METHODS AND DATA PREPARATION

Beaver Demography

We estimated abundance of active beaver colonies via aerial surveys conducted in 21 of the 47 years between 1962 and 2009. All surveys were conducted within a period spanning three to five days in mid to late October after leaves had fallen from deciduous trees and before snow covered the ground or ice covered the lakes.

The surveys involved flying NW-SE transects across the western region of Isle Royale, where beaver habitat is relatively rare. For the eastern and central regions, where beaver colonies are more common, the plane flew over all drainages (which run NE-SW). The plane circled back when the observer felt the need for a longer view to detect and record a colony. Finally, because colony density was especially high in the small area at Isle Royale's northeast end, that area was flown twice.

A colony was judged active on the basis of various sign, typically a lodge and food cache. Other signs taken to represent an active colony included: freshly peeled sticks, newly cut trees or shrubs, canals, fresh mud on a lodge, recently repaired dam, or sometimes a cache without a lodge (Hay 1958; Payne 1981; Brown & Parsons 1982; Swenson et al. 1983). For the analyses below, we used only that proportion of the population associated with a food cache as this provided the most assurance for colony presence. In a typical year, 0.85 (SE = 0.15; $P < 0.001$, single sample t -test, $n = 20$) of the annual number of colonies were associated with food caches. Details about the methods and results of these surveys are described in Romanski et al. (*in review*, see Chapter 1).

We assumed that growth rate of the beaver population is equal to the growth rate in the number of colonies so long as the mean colony size did not change over the span of time during which the growth rate is calculated. Because the colonies were not censused annually, we were only able to calculate the mean annual growth rates for period i , where period i was typically two years in duration (see Fig. 2-2). Specifically, we calculated the

mean annual growth rate, a fractional increase or decrease in abundance, for period i as (Dennis et al. 1991):

$$r_i = \ln[C_{t+i}/C_t]/\sqrt{t_{i+1} - t_i}, \quad \text{Eq. 1}$$

where C_t is the number of colonies in year t .

Wolf Demography

The wolf population was censused annually between 1958 and 2009 from a fixed-wing aircraft during January and February. Confidence in census accuracy is high because entire wolf packs are often visible at a single location and time and we make several complete counts during each winter. These estimates of wolf abundance have also been published and analyzed elsewhere (e.g., Vucetich and Peterson 2004b).

Moose demography

Moose abundance was estimated annually from 1999 to 2009 by aerial survey using fixed-wing aircraft (Peterson & Page 1993). From 1958 to 1998 moose abundance was estimated by cohort analysis, similar to that described by Solberg et al. (1999). For additional details see Vucetich and Peterson (2004a).

Climate data

During the study period (1962-2009), annual precipitation had been recorded at weather stations in northeastern Minnesota, approximately 40 km west of Isle Royale. We obtained these data from the Western Regional Climate Center (2010).

Stream flow had also been measured annually between 1965 and 2003 for Washington Creek, a USGS Hydrologic Benchmark station and one of the two major creeks on Isle Royale, located in the western region of Isle Royale (Mast and Turk 1999). Specifically, from this monitoring effort, we characterized annual stream flow as a mean of pooled monthly averages in cubic meters per second.

Scat Analysis

We collected wolf scats in 22 of the years between 1962 and 2009 (Table 2-1). The mean number of scats collected during each of these years was 190 (± 29 SE). We collected wolf scats from rendezvous sites and foot trails that were hiked between May and October. More often than not, a scat contained only one prey item, consequently, the number of prey occurrences per scat per annum did not differ significantly from mean number of scats collected (191 ± 14 , $P = 0.98$; paired t -test). Each scat was recorded as containing adult or calf moose, beaver or snowshoe hare (*Lepus americana*). This determination was made by identifying the macroscopic properties of hair that characterize each prey species. Our equation for interpreting scat occurrences does not incorporate non-mammalian food items (*see below*). Therefore, seeds, vegetation and

unknown scat occurrences were removed from the annual sample of scat occurrences prior to analyses.

To convert these observations into estimates of the proportion of each year's wolf diet (in terms of biomass) that is beaver, we used a technique developed by Floyd et al. (1978). The first step in that technique is to estimate the biomass of prey that each scat represents, given the body size of the prey. Specifically, we made this conversion by using this equation $K_j = 0.439 + 0.008M_j$, where K_j is the kilograms of prey species j that each scat represents, and M_j is the body size (in kilograms) of species j (Weaver 1993). For this equation, we used mean mass of 12 kg for beaver, 262.5 kg for adult moose, 45 kg for calf moose, and 1.2 kg for snowshoe hare (Thurber and Peterson 1993). The next step is to multiply the kilograms of prey per scat for each species j by the proportion of scats containing species j . Dividing the relative weight, the total weight (kg) of species j in the annual scat sample, by average weight of species j yielded relative number of individual moose calves, beaver, and snowshoe hare per adult moose (Floyd et al. 1978). From these estimates of biomass per prey species, we estimated the proportion of wolf diet that is beaver.

Predation Rates

Annual predation rate (PR_t) is the proportion of beavers in year t that were killed by wolves. We estimated PR_t from estimates of the number of wolves in the population in year t (W_t), the proportion of wolf diet in year t that was beaver (PB_t), mean number of beavers in each colony (CS_t), and C_t . Specifically, we estimated PR_t as:

$$PR_t = \left((3.25z_tW_t) \frac{365}{2} \frac{PB_t}{12} \right) / C_tCS_t \quad \text{Eq. 2}$$

where the numerator represents the number of beaver killed annually and the denominator represents the size of the beaver population. Because 3.25 kg of prey represents the minimum daily energetic requirements of a wolf (Mech and Boitani 2003), the quantity $3.25W_t$ represents a conservative estimate for average amount of food that wolves would consume daily. The variable z_t is an adjustment factor that accounts for annual variation in the wolves' kill rate (*see below*). Because the quantity $365/2$ represents the fraction of the year that wolves feed on beavers (i.e., May-October), the first two terms of the numerator represent the kilograms of prey that the wolf population consume annually. Multiplying this quantity by PB_t yields the kilograms of beaver consumed annually. Dividing this quantity by 12 kg (the mean mass of a beaver) yields an estimate of the number of beaver killed by wolves annually. We assumed that the mean colony size was 6.4 beavers (Shelton 1966).

To account for annual variation in kill rate, we predicted kill rate (kills/wolf/day, measured annually from 1971 to 2009 each January and February) from the ratio of moose to wolves. Previous work indicates that the ratio of moose to wolves is the most important predictor of kill rate (Vucetich et al. 2002). Specifically, the most parsimonious relationship between these variables is linear, $kill\ rate_t = 1.41 \times 10^{-2} + 1.54 \times 10^{-4}(M_t/W_t)$ ($R^2 = 0.49$, $P < 0.01$), where M_t is moose abundance in year t . Moreover, the mean kill rate for the period 1971-2009 is 2.29×10^{-2} . If 3.25 kg/wolf/day

represents a typical kill rate, then $3.25z_t$, should be a reasonable indicator of how kill rate varies with the ratio of moose-to-wolf, where z_t is $[1.41 \times 10^{-2} + 1.54 \times 10^{-4}(M_t/W_t)]/2.29 \times 10^{-2}$. For the Isle Royale data for z_t ranges from ~ 0.71 to ~ 1.6 . Even if one or more of the constants in Eq. 2 were inaccurate, PR_t would still be a useful index of annual predation rate because variation in the PR_t is determined by changes in wolf abundance, beaver colony abundance and the proportion of the wolf diet that was beaver for any given year.

Reconciling Predation Rate and Growth Rate

One of our interests is to assess the relationship between predation rate (PR_t) and growth rate (r_t) (*see Analysis*). This assessment is complicated, however, because PR_t is estimated each year for which an estimate of C_t is available, and these estimates of PR_t apply only to that particular year. Similarly, most estimates of r_t represent an average annual growth rate for a two-year period. However, we have two of three values necessary to calculate PR_t annually, specifically, the proportion of wolf diet that is beaver (PB_t) and the number of wolves (W_t). To capture PR_t in those years for which C_t was not directly observed, an estimate of colony abundance for that year between any particular two-year interval was derived by calculating the mean using observed abundances from those years that bound the interval. For example, in 1978 C_t was 129 and C_t for 1980 was 83, therefore, a C_t estimate for 1979 would be 106 $([129 + 83] / 2 = 106, \text{ see Table 2-1})$.

Similarly, r_i for the same year bounded by an interval can be estimated using the C_t estimate and Eq. 1. For example and again for 1979,

$$r_{1979} = \ln[83_{1980} / 106_{1979}] / \sqrt{1980 - 1979} = -0.244.$$

ANALYSIS

To better understand how bottom-up processes might affect beaver population dynamics, we assessed the extent to which colony abundance was correlated across Isle Royale's three distinct regions (i.e., eastern boreal forest region, central region, and the western northern hardwood forest region). Specifically, we estimated Pearson's product-moment correlation coefficient, r , to assess this relationship for the three combinations of observational pairs of beaver colony abundance per paired forested region (Zar 1984).

For example,

$$r = \frac{\frac{\sum X_{west} Y_{central}}{N} - (\frac{\sum X_{west}}{N})(\frac{\sum Y_{central}}{N})}{\sqrt{\frac{\sum X_{west}^2}{N} - (\frac{\sum X_{west}}{N})^2 * \frac{\sum Y_{central}^2}{N} - (\frac{\sum Y_{central}}{N})^2}} \quad \text{Eq. 3}$$

where X_{west} is the number of beaver colonies in the western region, $Y_{central}$ is the number of beaver colonies in the 1936 burn area, and N is the number of observational pairs of data. If beaver dynamics are strongly influenced by the trajectory of forest succession, then beaver dynamics on Isle Royale should be asynchronous among the

three regions of Isle Royale because the three regions have been following different trajectories in forest succession.

If beaver dynamics are well-correlated among the regions, then we might expect any of three processes could be responsible for synchronizing dynamics across these regions: climate, dispersal and predation. Though data do not exist that would allow us to directly assess the influence of dispersal, we are able to assess climate and predation. To assess the potential influence of climate on beaver colony growth rate we employed regression analysis using both mean annual precipitation and the mean annual stream flow as predictor variables. These two variables ought to represent the inter-annual variation in the amount of water available for use and impoundment by beavers. Water is an important requisite for food storage, foraging, escape from predators and lodge construction (Müller-Schwarze and Sun 2003).

We also aimed to assess two aspects of beaver predation: (i) how are beaver dynamics affected by predation, and (ii) what factors determine whether predation will be relatively high or low? With respect to the first goal, we used regression to assess the relationship between predation rate and growth rate of beaver colonies. If predation is an important aspect of beaver population dynamics, then we would expect beaver colony growth rate to decline with increasing predation rate.

With respect to the second goal, we used regression to assess whether predation rate is more influenced by the abundance of wolves or climate. If predation rate is an important top-down process, then wolf abundance would be the strongest predictor of

predation rate. If precipitation and stream flow, our surrogates for water availability, are positively associated beaver colony growth rate and if we accept that dispersing beavers are more prone to predation, then climate could be an important predictor of predation rate (decreasing water availability increases predation risk).

Finally, to better understand the extent to which predation is a stabilizing force on beaver dynamics, we assessed the relationship between beaver colony abundance and predation rate via regression. If predation rate tends to increase with beaver colony abundance then predation rate has a stabilizing influence on beaver dynamics. If abundance and predation rate are inversely related, then predation would be a destabilizing force on beaver dynamics (Ives et al. 2005).

Assessments of how predation rate (Eq. 2) relates to beaver colony growth rate (r_t), beaver abundance (C_t), and wolf abundance (W_t) are motivated by an interest to make inferences that are closely related to ecological theory (Ives et al. 2005). However, although Equation 2 may be ecologically justified, it does present a statistical challenge because PR_t is a function of W_t and a correlation between these variables could represent a statistical artifact. Nevertheless, careful scrutiny of relationships can avoid spurious interpretations (*see* Discussion). It may also be valuable to assess relationships that are not so statistically complex, even if these relationships are not so closely linked to ecological theory. For this reason, we used regression to assess how PB_t , the proportion of wolf diet in year t that was beaver, is related to C_t , W_t , and r_t . These data were gathered from independent field methods, and as such, are statistically independent.

All analyses described above were performed in the statistical package R (version 2.10.1, R Development Core Team 2009).

RESULTS

Population Demography

Island-wide, temporal trends in abundances for beaver colonies and wolves are presented in Fig. 2-2. Mean beaver colony abundance combined with other associated sign confirming beaver presence was 149.9 (SE = 14.2, $n = 20$). As stated previously, we used only that proportion of observed beaver colonies which was associated with a food cache (C_i) to calculate predation rates using Eq. 2 (0.845 ± 0.004 , $n = 20$, [mean $\pm$ SE]). The mean number of sites whose beaver sign was associated with a food cache, hereafter referred to as beaver colonies, did not differ from total observed abundance (130.9 ± 12.6 ; paired t -test, $P = 0.25$). Mean annual beaver colony growth rate, r_i , trended downward and varied considerably for the period (-0.0069 ± 0.04 , $n = 20$). For those years where beaver colony abundance was observed, the corresponding average wolf abundance approximated average wolf abundance for the entire period from 1962 to 2009 (24.3 ± 2.2 , $n = 22$ and 23.7 ± 1.3 , $n = 48$, respectively; paired t -test, $P = 0.81$).

Climate

Mean annual precipitation for the study period was 72.1 cm (± 1.2 SE; interquartile range = [67, 75], $n = 48$). The mean annual stream flow of pooled monthly averages between 1965 and 2003 was $0.45 \text{ m}^3/\text{sec}$ (± 0.02 SE; interquartile range [0.34,

0.50], $n = 39$). Water availability, as represented by precipitation and stream flow, appeared quite stable over the period. However, inter-annual variation was considerable and a slight downward trend apparent (Fig. 2-3)

Scat Analysis

Estimates of wolf diet from scats collected annually, including: percent occurrence of beaver in scat, kilograms of beaver in the annual scat sample, percent biomass (proportion of wolf diet that was beaver), and relative number of beaver consumed per adult moose are shown in Table 1. We omitted data from year 2009 as a statistical outlier from any forthcoming analyses regarding predation rate. For this year the importance of beaver is artificially inflated because no moose occurrences were observed in the scats collected. Mean annual percent scat occurrence for beaver was 29.0% (± 2.9 SE, $n = 37$). Mean proportion of beaver in wolf diet for the period, presented as percent biomass ($PB_{ave} \times 100$), was 13.8% (± 1.8 SE, $n = 37$) and changed little from the 14% reported by Thurber and Peterson (1993) despite more than doubling sample size ($n = 37$ vs. $n = 15$). Relative number of beaver consumed per adult moose differed among sampling intervals (6.1 ± 1.2 SE; interquartile ranges [1.4, 8.0]; $\chi^2 = 247.5$, $df = 33$, $P < 0.001$, Chi-squared test).

Predation Rate

The proportion of the annual beaver population consumed by wolves (PR_t), for both directly observed and estimated beaver colony abundance, for the period averaged 0.163 (± 0.02 SE; interquartile ranges [0.069, 0.217] ; $n = 34$; *see* Fig. 2-2 and Table 2-1). Mean predation rate for only those years where beaver colony abundance was observed directly (0.165 ± 0.02 SE; interquartile ranges [0.073, 0.217]; $n = 20$) was similar to the pooled sample of observed and estimated beaver colony abundance ($P = 0.96$, paired t -test). Using predation rates, we calculated the number of beaver consumed per year ($C_t \times 6.4$ beaver per colony $\times PR_t$) and yielded a mean of 137.4 beavers consumed annually for the study period (± 18.9 SE; interquartile ranges [50, 233]; $n = 34$; *see* Table 2-1).

Analysis

Beaver colony abundance correlated well throughout the study period between each of the paired combinations of the three, distinct forested communities ($r_{(\text{west-east})} = 0.812$, $t = 5.729$, $df = 17$, $p\text{-value} < 0.0001$; $r_{(\text{west-burn})} = 0.783$, $t = 5.1852$, $df = 17$, $p\text{-value} < 0.0001$; $r_{(\text{burn-east})} = 0.762$, $t = 4.8549$, $df = 17$, $p\text{-value} = 0.00015$, Pearson's product-moment correlation, Fig. 2-4).

Our climate variables representative of water availability did not importantly explain variation in beaver colony growth rate. Both mean annual precipitation ($R^2 =$

0.03, $P = 0.45$) and stream flow ($R^2 = 0.04$, $P = 0.48$; Fig. 2-5) failed to significantly predict variation.

Beaver colony growth rate did not respond negatively to predation rate for the period ($R^2 = 0.02$, $P = 0.40$; Fig. 2-6A) as expected. Predation rate was not influenced by water availability, predicted by mean annual precipitation or stream flow ($R^2_{precip} = 0.06$, $P = 0.17$ and $R^2_{flow} = 0.08$, $P = 0.14$; Fig. 2-6 A,B), suggesting dispersal may not have been prompted by lack of available water and the subsequent increasing predation risk realized. Wolf abundance explained 26% of the variation in predation rate ($P = 0.002$; Fig. 2-6D).

Variation in the proportion of wolf diet comprised of beaver (PB_t) was not strongly influenced by either number of wolves ($R^2 = 0.01$, $P = 0.40$) or beaver colony growth rate ($R^2 = 0.02$, $P = 0.40$). However, beaver colony abundance explained 29% of the variation in the proportion of diet that was beaver ($R^2 = 0.29$, $P = 0.01$). We log transformed (base 10) beaver colony abundance to reflect the curvilinear response of predation and back-transformed to express this relationship ($R^2 = 0.30$, $P < 0.0001$; Fig. 2-7A, see Table 2-2 for detailed results of all regression analyses).

Discussion

Predator-prey interactions and their role in ecosystem function and diversity are important and complex, and have been appreciated as such (Duffy et al. 2007). However,

less appreciated, are the varying time scales at which these interactions exert themselves. The conception of these processes as largely driven from the “top-down”, “bottom-up”, the abiotic environment, or any combination thereof could be misinterpreted without recognition of appropriate time scales. Our understanding of predator-prey interactions on Isle Royale benefit from articulation of the “4th” dimension, time. Although we cannot go back in time; provided we keep looking in the present for a sufficient period of time, we may look back on time and appreciate yesterday’s chaos with historical perspective. It is under this framework that we move forward.

With regards to forest succession and influences of bottom-up processes on beaver population dynamics, interpretation of our results suggests that the synchronicity of abundances in the three distinct forest communities imply that on a larger spatial scale over a multi-decadal period, bottom up forces are not solely influential. However, contemplating the relative distribution of abundances through time, we suspect that the underlying geology coupled with forest succession has set the stage for this distribution on Isle Royale (*West* = 23.32 ± 3.50 , *Central* = 46.47 ± 5.35 , and *East* = 82.05 ± 7.06 ; [Mean $\pm$ SE]; Fig 2-4D). What has traditionally been considered “quality” beaver habitat, both on Isle Royale and elsewhere (Shelton 1966, Jenkins 1980, and Fryxell and Doucet 1993) is and has been lacking in the western northern hardwoods forest region (Linn 1957, Belovsky 1984). Old-growth stands of sugar maple and yellow birch have persisted and are expanding in this portion of Isle Royale (Janke et al. 1978, Sell 2007). However, beaver trends here are synchronized with the remaining portions of the island. Beaver are “choosy generalist” and diet constraints have largely been attributed to local

availability (Müller-Schwarze and Schulte 1999), and secondarily to nutritional quality and digestibility (Fryxell and Doucet 1993). Consequently, over short time-scales, local resource depletion can lead to a population always in transition (Fryxell 2001). Using data from the last four years of our study period, those years for which we are most confident about estimates of colony abundance (Romanski et al. *in review*) we determined a mean annual rate of abandonment at ~ 60% (Peterson and Romanski 2009). Local resource depletion is occurring on a short, time-scale (2-4 yrs) island-wide and rates of abandonment reflect this, however this trait appears to be typical for other populations (Fryxell 2001, Hyvonen and Nummi 2008). Nevertheless, does this response increase predation risk?

Forest succession and structure on Isle Royale is greatly influenced by moose herbivory (for *a review see* Jordan et al. 2000, Pastor et al. 1998, Sell 2008, DeJager and Pastor 2009, DeJager et al. 2009). This prolonged level of intense herbivory undoubtedly affects beaver population dynamics. Competitive exclusion of beaver by large ungulates has been shown in other systems (Wolf et al. 2007, Hood and Bayley 2008). Additionally, the cumulative effect of moose and beaver herbivory may be affecting beaver population dynamics. In one study area on Isle Royale, beaver significantly reduced aspen density from 140 stems/ha to 27 stems/ha while moose concurrently and preferentially selected aspen twigs over a 21 year period (Moen et al 1990). Elsewhere, the selection of large aspen trees by beaver opens the canopy to encourage recruitment and stand replacement (Ritchie 1983). However, moose density on Isle Royale is considered high (Vucetich and Peterson 2004a) and consequently moose have effectively

browsed most deciduous saplings or twigs, thereby decreasing recruitment (Jordan et al. 2000). The combined effects of beaver and moose herbivory may hasten conversion to conifer stands without stand-replacing disturbance (e.g., fire) and ultimately erode suitable beaver habitat (Barnes and Mallik 2001). Despite the exceptional fecundity exhibited by beaver and the ability for a population to expand rapidly (Hartman 1994), poor habitat quality has led to reduced reproductive rates (Gunson 1970). Reciprocating effects of foraging, both moose and beaver herbivory, may negatively influence beaver population dynamics on Isle Royale.

Dispersal of beaver may not be influenced by resource depletion alone, and when densities are low, dispersal of yearlings will occur (Hartman 1997). Density, number of active colonies per km of stream, is relatively low on Isle Royale and this could precipitate dispersal (0.52 colonies/km, reported ranges ~0.40 to 1.09; Hartman 1997, Muller-Schwarze and Sun 2003). Water plays a crucial role in many aspects pertaining to the natural history of beaver, including dispersal. The importance of water with respect to predation is notable. Basey and Jenkins (1995) demonstrated that beaver minimize the predation risk to energy return ratio by consuming the stripped bark of aspen in water, thus trading a profitable return on energy for the security water provides. The fear of predation is important for shaping dynamics in other predator-prey interactions and ultimately the landscape (Brown 1999, Launde et al. 2010). In the absence of available water, dispersal in search of, or for the lack of, water might increase risk to predation. We were unable to implicate lack of available water as an abiotic

process influencing either population dynamics or susceptibility to predation over a multi-decadal period (Fig. 2-5, Fig. 2-6 Panels B and C).

Using colony density per unit area (km^2) data from across Quebec, Canada and multi-variate and single variable models along with a species-climate envelope model, Jarema et al (2009) demonstrated that a single predictor model showing density exhibited a positive response to increasing potential evapotranspiration (PET) over a growing season ($R = 0.56$, $P = 0.000$). The authors' predicted beaver density to increase in response to predictions under current global change models. In this same study, predation, number of wolves per km^2 , explained only 2.9% of the variation in a single predictor model ($P = 0.039$). However, at the inter-annual scale, short-term extremes in climate may have influenced predation in our system. In 1976, 16% of wolf diet consisted of beaver (PB_t), ~3% above the long term average, and our observed minimum in mean annual precipitation, 53 cm, occurred. Coupled with high numbers of wolves, lack of available water may have exacerbated already high risk to predation. Beaver colony abundance dropped precipitously during the period from 286 colonies in 1974 to 129 in 1978. Unfortunately, beaver colony abundance was not estimated in 1976 and a calculation of predation rate (PR_t) cannot be derived. It may be that inter-annual impacts to beaver population dynamics from lack of available water, an abiotic surrogate, are buffered temporally by beavers' ability to impound and in a sense, harvest water (Rosell et al 2005). Alternately, the resolution of our data (annual scale), could have been too coarse to implicate lack of available water as impetus for dispersal and subsequent increased predation risk.

Wolf predation served as a stabilizing force on beaver colony abundance on Isle Royale between 1962 and 2009 (Fig 2-7A). Initially, in the period prior to 1978, beaver colony abundance increased following a decline likely attributable to a regional outbreak of tularemia and secondarily, the concurrent arrival of wolves in 1948 (Shelton 1966). By 1974, peak beaver colony abundance had been obtained ($C_t = 286$, Fig. 2-2, Table 2-1) and briefly thereafter, wolf abundance peaked as well (1980, $W_t = 50$). Predation rate (a functional response) responded to predator density in this short, or fast, time scale and had a stabilizing affect (Fig. 2-6D; $R_2 = 0.26$, $P = 0.002$) (Abrams and Ginzburg 2000, Vucetich et al 2002). By 1980 beaver colony abundance decreased by ~200 colonies or 70% from that of 1974. Similarly, beaver colony abundance declines during a period of high wolf abundance between 1990 and 2000 (Fig. 2-2). We are aware of only one other study, 5 years in duration, which documented a similar response. Potvin et al. (1992) measured a 30% drop in density of beaver colonies in Quebec following the stoppage of wolf control measures. From 1974 to 1980, a discrete and short time scale, beaver colony abundance was influenced by the top-down process of wolf predation.

Disease, often a short-lived perturbation, can drive ecosystems with long-term effects (e.g. Hoklo et al. 2009). Despite being an island, Isle Royale is not immune to disease and an outbreak of canine parvo-virus reduced the wolf population from 50 to 12 in just two years between 1980 and 1982, and importantly changed predator-prey dynamics with moose whereby top-down influences were diminished thereafter (Wilmers et al. 2006). Similarly, beaver predation rates responded negatively to this perturbation and number of beaver colonies increased (83 in 1980 to 204 in 1986, Table

1). Following this event and throughout the remainder of the study period, predation likely decoupled and became a destabilizing force with mixed effects on the population dynamics of beaver (Abrams and Ginzburg 2000), or in other words, the strength of top-down influence diminished.

In a novel way, beaver were a bottom-up influence on the wolf population during a period of high wolf abundance and a concurrent low moose to wolf ratio (Vucetich et al 2002). As such, beaver subsidized the atypically high number of wolves. Between 1974 and 1980, the same period discussed previously, average number of wolves was a full 16 individuals higher than the study period average (40 vs. 24) and the moose:wolf ratio was greatly reduced (26 between 1974-1980 and 57 for the study period). Anderson (1999) reported an equivalent relationship in which beaver became an important alternate prey during low ungulate density. Increasing importance of alternative prey can be characteristic of apparent competition.

Holt and Lawton (1994) use the terms focal (moose) and alternate (beaver) in a review of apparent competition and suggest complicated relationships between one predator, and a focal prey and an alternate prey, vary on short and multi-generational time scales and often manifest quite differently at each scale. We offer evidence for this complexity on both scales in support of our implication that beaver population dynamics were an influence (bottom-up) and influenced themselves (top-down) on a short-term time scale in its interactions with the wolf population. Numerically and for the short-term, both moose and beaver colony abundance responded negatively to 6-7 year period

of atypically high wolf abundance (Fig. 2-2, Table 2-1), and abundances increased shortly after the wolf population's crash from canine parvo-virus. Functionally, our relationship between beaver colony abundance (C_t) and the response in the proportion of wolf diet that was beaver (PB_t ; $R^2 = 0.30$, $P < 0.0001$; Fig. 2-7A), indicate beaver were an important prey item over a 50 year period for wolves. Theory predicts that when predators are limited by prey availability, alternate prey experience long-term negative-negative interactions via shared predation leading to species exclusion (Holt and Lawton 1994). Furthermore, the long-term decline in overall abundance and mean annual growth rate of beaver colonies may provide evidence for apparent competition (Fig. 2 and Table 2-1).

Beaver have returned to the landscape following near extirpation from trapping associated with the fur trade of the 19th and early 20th centuries (Müller-Schwarze and Sun 2003). However, ecosystem functions similar to those provided by beaver prior to European settlement may not be restored completely because in many instances they occur without the influences of predation. Although other predators consume beaver, wolf predation holds primacy where these two species overlap (Rosell et al. 2005). Here we have demonstrated important long and short-term impacts of wolf predation on beaver population dynamics. However, in the absence of wolves, how have the activities that have earned beaver the title “ecosystem engineer” changed? For example, it would seem natural to encourage the establishment of beaver to restore streams and stream processes (e.g., Albert and Trimble 2000). This may be appropriate, but what are the unintended consequences of beaver populations unchecked by predation? Can the effects of beaver

dams and activities: trap too much sediment, stabilize stream banks excessively, or increase herbivory to the point of altering succession inappropriately? These questions are likely not being addressed because little data exists regarding the impacts of predation on beaver population dynamics. Consider, for example, wolf predation has restored stream processes and landscape features, as well as, encouraged beaver activities in stream corridors at Yellowstone National Park by modifying elk behavior (Beyer et al. 2007). It is important to recognize that in this example all the pieces are present, including predation (Carrol et al. 2001).

Our results indicate wolf predation can be a strong top-down influence on beaver population dynamics, but the nature of this strength could be more importantly manifested over a short time scales and largely attributable to the number of wolves on the landscape, or predator dependent (Abrams and Ginzburg 2000). Conversely, the number of active beaver colonies predicted increasing predation rate in our system, suggesting that prey density can drive predation (Holling 1966). In conjunction with the complexities of wolf-moose-beaver interactions characterized by apparent competition (Holt and Lawton 1994), predation may be operating on long-term beaver population dynamics where we observed declining trends in abundance over a 48 year period. Surprisingly, our work is the first to comprehensively consider the role of predation in the population dynamics of beaver, an important ecosystem engineer. Recognition of the “4th” dimension, scaled for both fast (short-term) and slow (long-term) processes, has provided important insights that could not be appreciated otherwise. Clarifying the role of predation can inform management of restored beaver populations whose activities are

now being carried out in the absence of predation. Populations of beaver are predicted to expand with global climate change (Jarema et al. 2009) and predation could play a key role in keeping growing populations in check if predators are returned to the landscape as well. In this way, ecosystem functions and diversity are more fully restored.

Acknowledgements

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Table 2-1. Population trends of wolves, moose, and beaver, and measurements of beaver predation by wolves as calculated using a linear equation to interpret scat occurrences in wolf feces (Weaver 1993) collected on Isle Royale National Park, Michigan, USA, between 1962 - 2009.

Year	Number of Wolves W_t	Number of Moose M_t	Number of Beaver Colonies C_t	Beaver Colony Growth Rate r_t	Scats Collected	Scat Occurrences*	% Scat Occurrence Beaver	kg [†] Beaver in Scat Sample	% Biomss Beaver PB_t	No. Beaver Per Adult Moose	Predation Rate PR_t	No. Beaver Consumed Annually
1962	23	579	117	0.181	475	497	13.2	20.9	3.5	11.0	0.042	31.6
1973	24	1260	213	0.295	554	830	50.6	224.7	28.1	13.6	0.234	319.0
1974	31	1246	286	-0.398	443	534	39.3	110.2	19.2	7.9	0.141	258.5
1975	41	1175	-	-	650	536	48.4	154.1	17.0	4.5	-	-
1976	44	1099	-	-	641	611	47.0	161.6	16.2	4.3	-	-
1977	34	967	-	-	157	144	58.4	48.2	24.7	7.5	-	-
1978	40	854	129	-0.312	90	87	44.9	21.4	21.3	8.0	0.386	318.8
1979	43	866	106 ^{††}		393	372	19.3	40.7	8.7	3.3	0.203	138.0
1980	50	792	83	0.290	571	548	41.7	125.7	15.0	4.1	0.504	267.9
1981	30	767	104		70	67	37.7	13.9	24.6	24.0	0.431	287.0
1982	14	779	125	0.134	128	132	17.5	12.8	8.1	3.2	0.069	55.5
1983	23	829	138		164	130	27.5	21.9	18.8	31.5	0.208	183.7
1984	24	928	151	0.213	134	129	47.4	33.7	24.9	10.8	0.268	258.9
1985	22	976	178		50	22	50.0	9.6	24.9	9.2	0.218	247.8
1986	20	1011	204	-0.014	207	207	13.0	14.4	3.4	0.8	0.024	31.8
1987	16	1040	202		31	24	62.1	9.6	53.3	-	0.344	444.8
1988	12	1109	200	-0.090	71	69	40.3	15.5	12.8	3.3	0.074	94.5
1989	12	1257	188		75	78	56.4	23.5	24.5	7.5	0.160	192.3
1990	15	1313	176	-0.177	130	136	54.4	39.6	26.0	9.0	0.206	232.6
1991	12	1500	157		243	198	27.4	58.3	13.9	5.8	0.119	119.5
1992	12	1708	137	0.000	141	138	39.9	29.4	16.5	5.1	0.174	153.0

Table 2-1., continued.

Year	Number of Wolves W_t	Number of Moose M_t	Number of Beaver Colonies C_t	Beaver Colony Growth Rate r_t	Scats Collected	Scat Occurrences*	% Scat Occurrence Beaver	kg [†] Beaver in Scat Sample	% Biomss Beaver PB_t	No. Beaver Per Adult Moose	Predation Rate PR_t	No. Beaver Consumed Annually
1993	13	1798	<i>137</i>		74	75	12.0	4.8	6.0	2.6	<i>0.068</i>	59.6
1994	17	2043	137	-0.048	104	102	4.9	2.7	1.9	0.6	0.026	22.9
1995	16	2145	<i>133</i>		168	173	12.1	11.2	4.2	1.2	<i>0.059</i>	50.3
1996	22	2435	128	-0.241	15	15	20.0	1.6	5.8	1.4	0.103	84.4
1997	24	697	<i>110</i>		314	307	27.7	45.5	15.3	9.1	<i>0.223</i>	157.3
1998	14	808	91	-0.156	217	192	29.2	30.0	18.2	14.3	0.229	133.4
1999	25	873	82		121	174	25.9	24.1	6.9	1.6	<i>0.144</i>	75.7
2000	29	942	73	-0.010	26	39	20.5	4.3	5.6	1.4	0.148	69.0
2001	19	1015	73		9	5	0.0	0.0	0.0	0.0	<i>0.000</i>	0.0
2002	17	1160	72	-0.258	42	53	22.6	6.4	6.3	1.5	0.121	55.7
2003	19	1026	<i>61</i>		186	178	3.9	3.7	1.4	0.4	<i>0.031</i>	12.2
2004	29	750	50	0.538	101	94	9.5	5.4	3.4	1.0	0.120	38.3
2005	30	540	<i>79</i>		135	107	4.7	2.7	2.1	0.9	<i>0.045</i>	22.8
2006	30	450	107	-0.195	141	117	6.8	4.3	4.7	-	0.073	49.8
2007	21	385	88	0.066	32	37	18.9	3.7	13.9	-	0.189	106.3
2008	23	650	94	-0.066	103	98	18.4	9.6	10.7	7.8	0.163	98.2
2009	24	530	88	-	31	21	50.0	0.5	54.4	-	0.875	492.9

Notes:

(*) Scat occurrences can be less than total number of scats because fruit, vegetative material, and unknowns were removed from analyses.

(†) Kilograms of beaver calculated using a methods prescribed by Weaver (1993). See *Field Methods and Data Preparation* for details.(††) Italicized values for beaver colony abundance and predation rate are calculated from an estimate of colony abundance. See *Field Methods and Data Preparation* for details.

Table 2-2. Results of regression analyses to assess the influences of abiotic processes and top-down control on beaver population dynamics from 1962 - 2009 in Isle Royale National Park.

Model	<i>df</i>	R^2	<i>P-value</i>	Figure (Panel)
$^{\dagger}PB_t = -0.586 + 0.346 (\log_{10} * \text{Colony Abundance})$	32	0.30	< 0.001	2-7(A)
$PB_t = -0.013 + 0.001(\text{Colony Abundance})$	32	0.29	< 0.01	2-7(A)
$\text{Predation Rate} = 0.012 + 0.007 (\text{Wolf Abundance})$	32	0.26	0.002	2-6(D)
$\text{Predation Rate} = 0.305 + 0.319 (\text{Stream Flow})$	26	0.08	0.13	2-6(C)
$\text{Predation Rate} = 0.447 - 0.004 (\text{Precipitation})$	32	0.06	0.17	2-6(B)
$\text{Growth Rate} = -0.285 + 0.573 (\text{Stream Flow})$	13	0.04	0.48	2-5(B)
$\text{Growth Rate} = -0.634 + 0.008 (\text{Precipitation})$	18	0.03	0.45	2-5(A)
$\text{Growth Rate} = -0.046 + 0.227 (\text{Predation Rate})$	32	0.02	0.4	2-6(A)
$PB_t = 0.148 - 0.001 (\text{Wolf Abundance})$	32	0.01	0.76	2-7(B)
$\text{Predation Rate} = 0.149 + 0.0001 (\text{Beaver Colony Abundance})$	32	0.01	0.78	2.6(E)
$PB_t = 0.166 + 0.885(\text{Growth Rate})$	32	0.001	0.82	2-7(C)

$^{\dagger} PB_t$ = the proportion of the wolf diet that is beaver from macroscopic analyses of wolf feces (see Table 2-1, % biomass beaver)

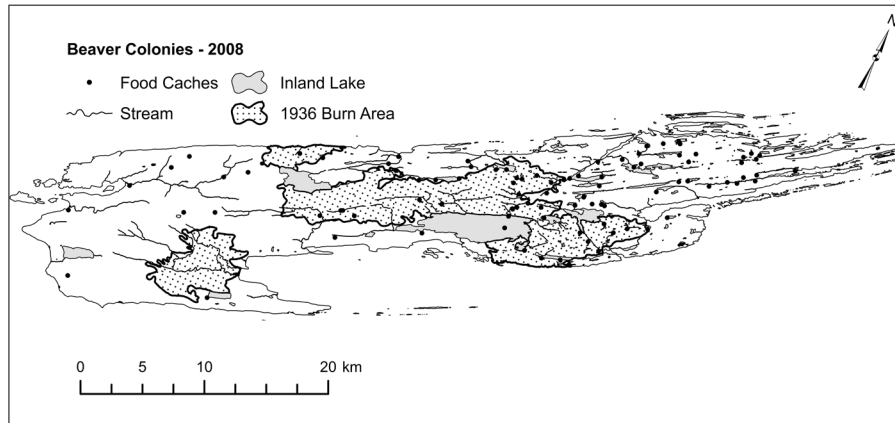


Fig. 2-1. Map of Isle Royale, Lake Superior, North America, showing the distribution of: (a) the distinct forested communities with the 1936 burn area (□) bisecting the boreal forest to the northeast and northern hardwoods to the southwest, and (b) a typical distribution of active beaver colonies (●) represented by data collected in 2008.

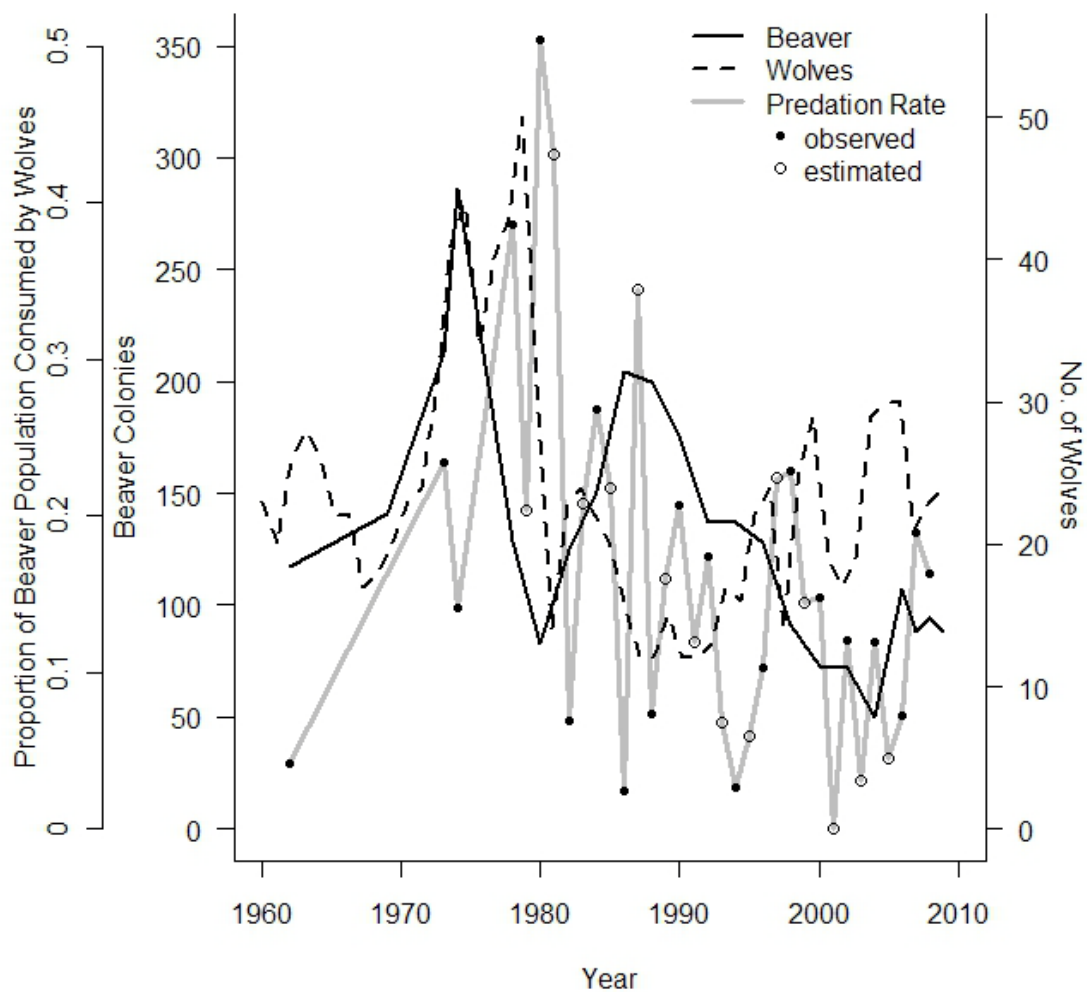


Fig. 2-2. The abundance of active beaver colonies (solid line) and wolves (dashed line), and predation rate (gray line), the proportion of the beaver population consumed by wolves annually, for both, directly observed beaver colony abundance (solid circle), $n = 20$, and estimated beaver colony abundance (open circle), $n = 14$, as determined by the mean of the two observed abundances bounding the estimate, between 1962 and 2009 for Isle Royale National Park, Michigan, USA.

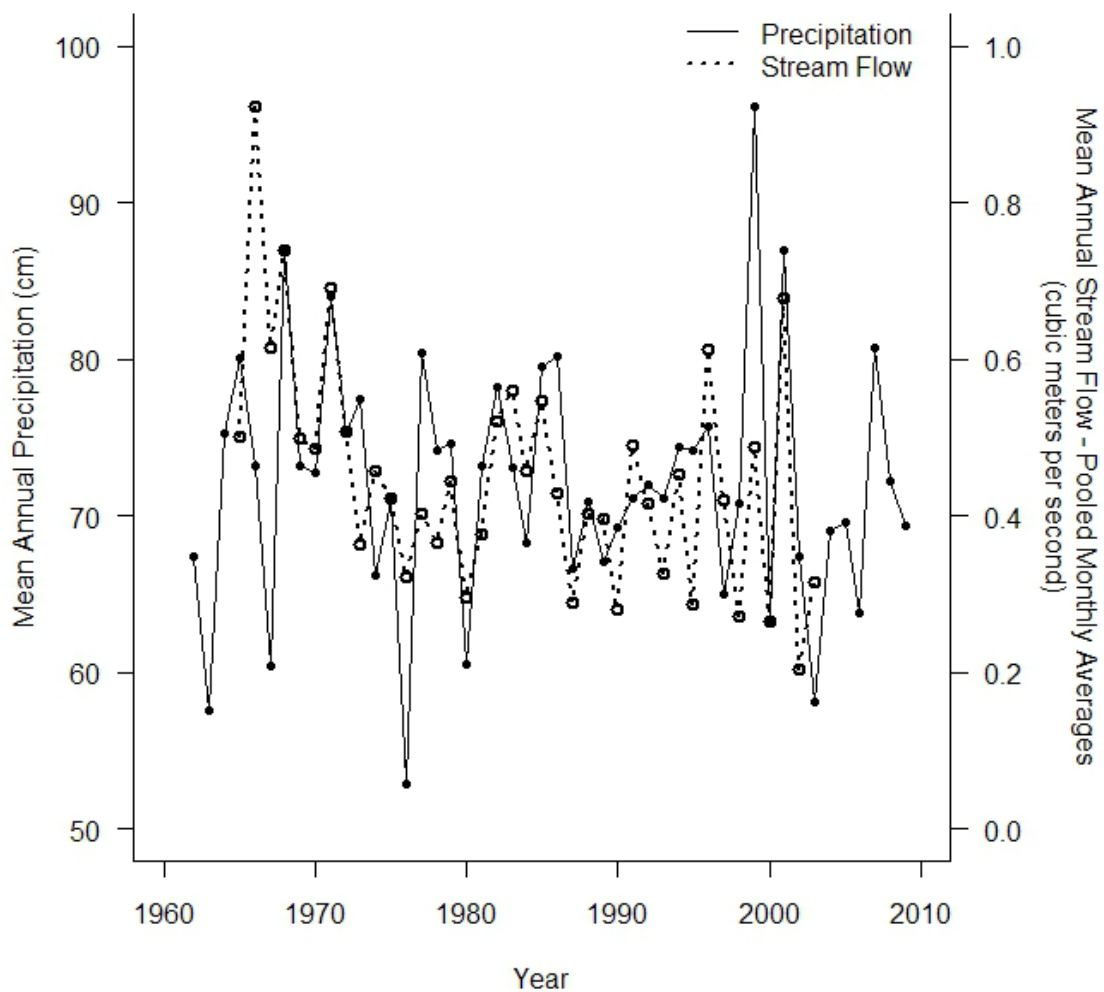


Fig. 2-3. Inter-annual variation in water availability for use and impoundment by beavers as represented by mean annual precipitation (solid line, solid circles) from 1962 to 2009 ($n = 48$) and the mean annual stream flow from pooled monthly averages (dotted line, open circles) for the period between 1965 and 2003 ($n = 39$) for Isle Royale National Park, Michigan, USA.

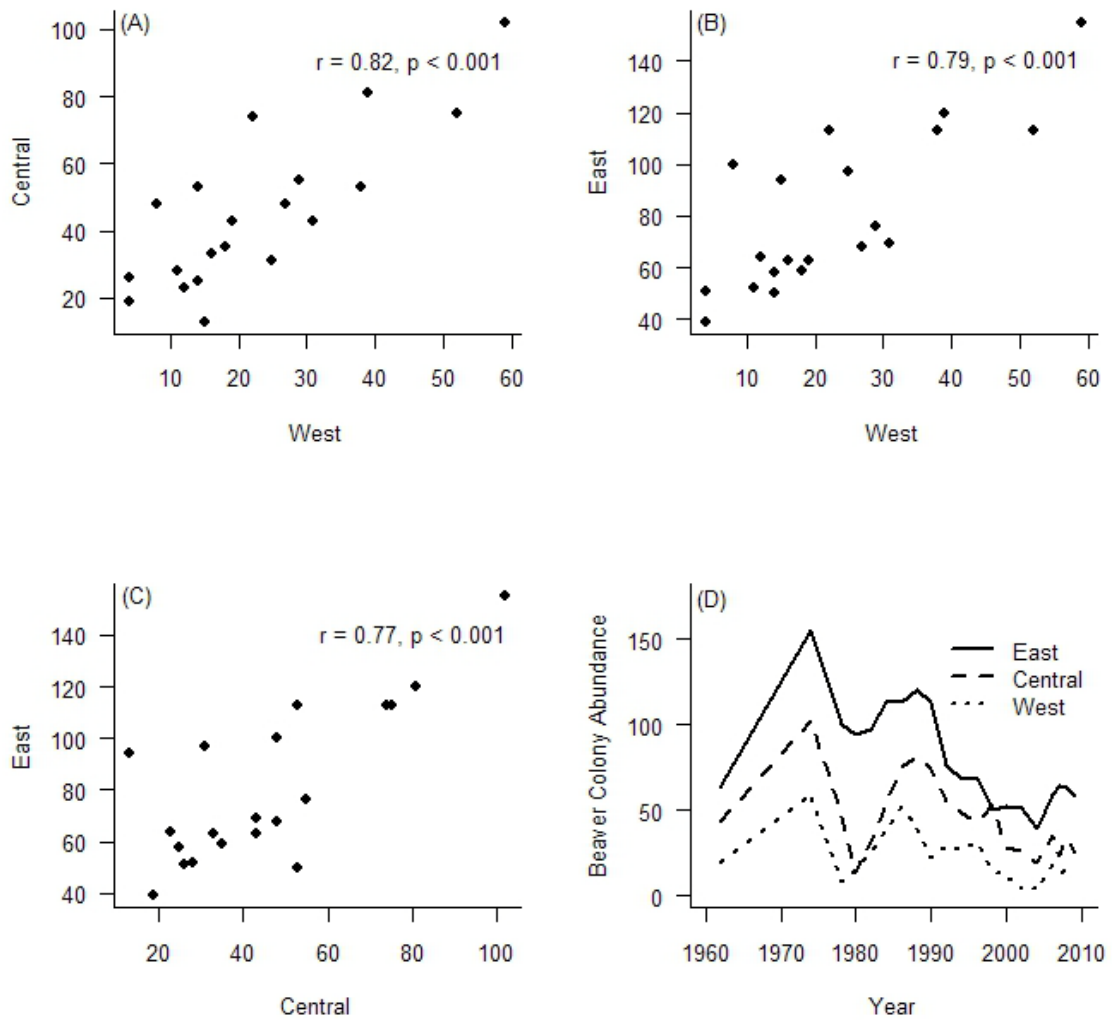


Fig. 2-4. Temporal correlation, using Pearson's product-moment correlation coefficient (r), of beaver colony abundance under three, distinct, forest succession trajectories (eastern boreal forest region, central 1936 burn area, and the western northern hardwoods forest region) on Isle Royale National Park, Michigan, USA, from 1962 to 2009 ($n = 20$).

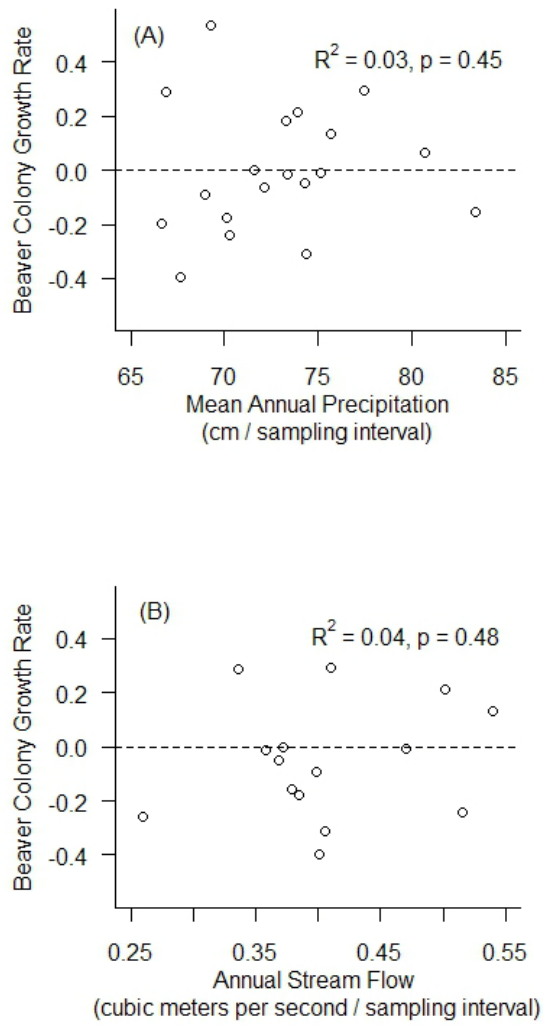


Fig. 2-5. Simple linear regression analyses relating beaver colony growth rate to water availability represented as (A) mean annual precipitation per sampling interval, centimeters ($n = 21$), and (B) mean annual stream flow per sampling interval, cubic meters per second ($n = 15$), in Isle Royale National Park, Michigan, USA, from 1962 to 2009.

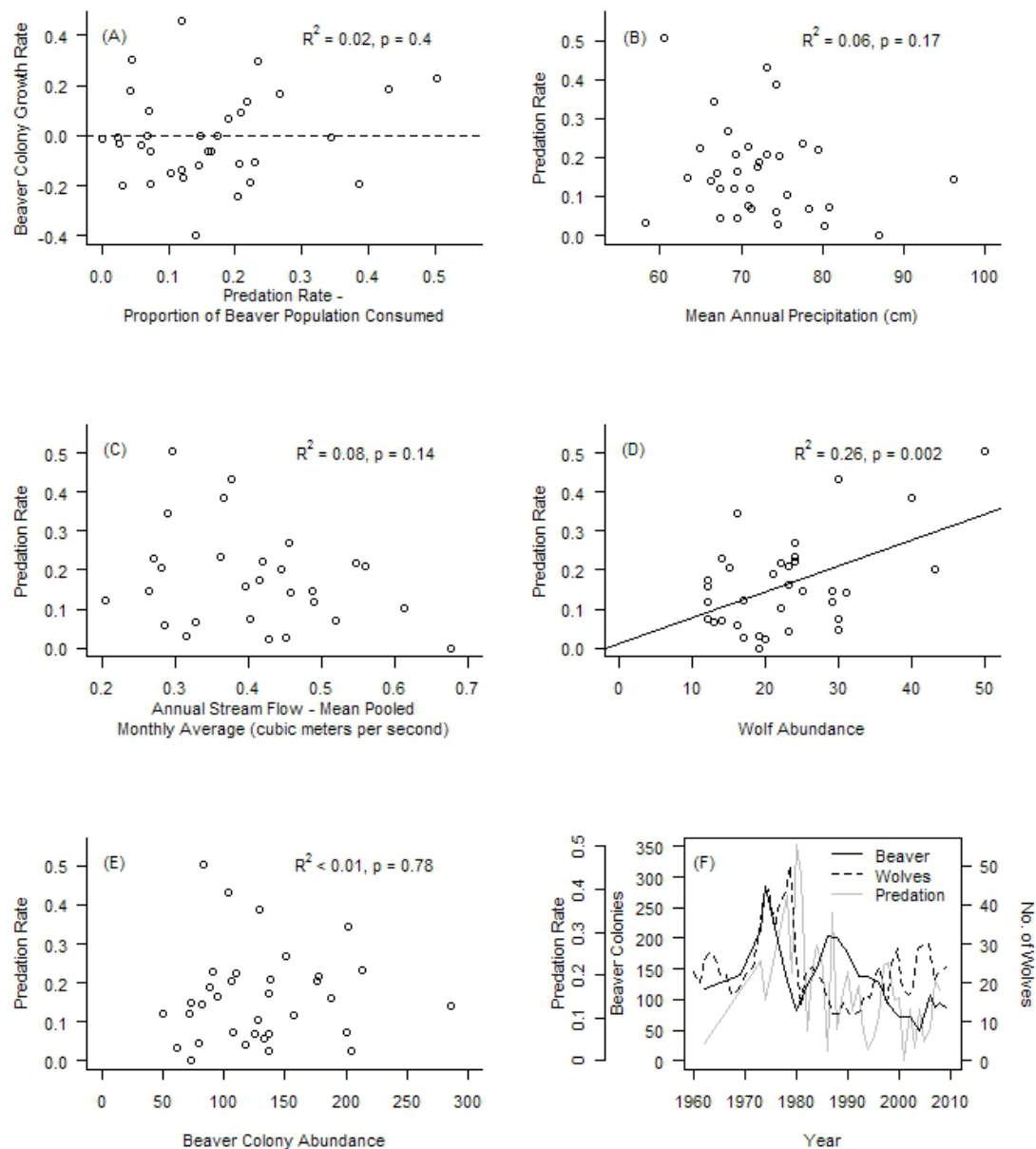


Fig. 2-6. Evaluations of predation as a top-down control of beaver population dynamics using simple linear regression analyses to investigate: (A) beaver colony growth rate as a function of predation rate ($n = 34$), and predation rate predicted by climate variables representing water availability, including; (B) mean annual precipitation ($n = 34$) and (C) annual stream flow as the mean of pooled monthly averages ($n = 28$); predation rate explained by (D) wolf abundance ($n = 34$) and (E) beaver colony abundance ($n = 34$); and (F) population and predation trends, from 1962 to 2009 for Isle Royale National Park, Michigan, USA.

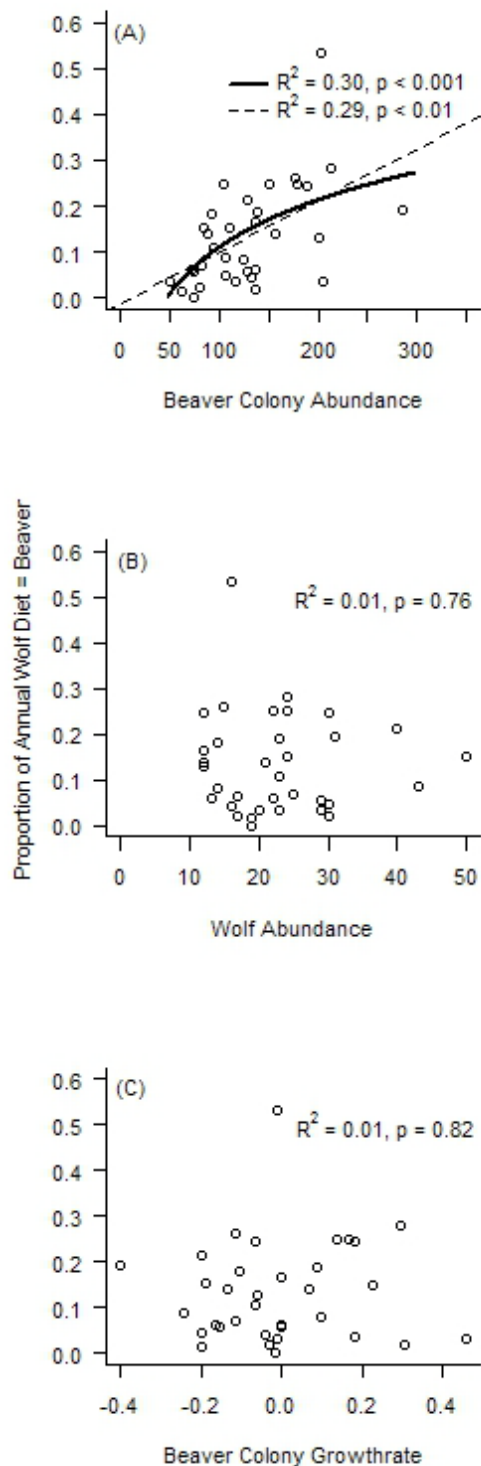


Fig. 2-7. Regression analyses to assess the relationship between the proportion of wolf diet that was beaver (determined by macroscopic inspection of wolf feces) and (A) beaver colony abundance, (B) wolf abundance, and (C) beaver colony growth rate, from 1962 to 2009 in Isle Royale National Park, Michigan, USA ($n = 32$).

CONCLUSIONS

The overarching purpose of my efforts in this thesis was to capture previous work and research and translate its importance to renew interests regarding beavers and beaver ecology on Isle Royale National Park. To this end, I have worked side-by-side with all the researchers who have played an important role in research to date. Initially we were caught off guard by the results of our most recent aerial surveys, 2006-2008 and thus, the first chapter of my thesis evolved. This chapter was required before other work could proceed in order reconcile previous estimates of beaver colony abundance. From this point, the second chapter was logical as wolf predation is well studied on Isle Royale with respect to moose, but in the literature predation and its effects on beaver ecology is surprisingly rare despite the importance of beaver as a keystone species and an importance component in the diet of wolves.

The first chapter in my thesis is a cautionary tale in the application of the double-count survey method. This method is applied in the aerial survey of numerous wildlife species and is important for validating population estimates. However, my colleagues and I have shown that all the assumptions must be strictly adhered to. Surprisingly, we did not become aware of our violation of the assumption that “all survey subjects are equally sightable” until after a modification of methodology. Specifically, we used two different styles of aircraft and flying styles. In the first two double-count surveys for beaver colony abundance, 1990 and 2002, we used a DeHavilland Beaver, a large, fixed-wing aircraft capable of holding the pilot and two independent observers. In subsequent

double-counts we used two smaller fixed-wing aircraft, each with a pilot and independent observer. Use of the larger aircraft grossly overestimated sightability but underestimated abundance. The DeHavilland Beaver is used prevalently for research but may be the improper tool. Depending on the application, smaller aircraft may provide substantially better observations and ultimately improved estimates of abundance for wildlife surveyed from aircraft. Comprehensively, our findings are a lesson for many applications of the double-count method, as it may not always be obvious when the assumption of equal sightability is being violated with as much consequence as we had experienced.

Predation, as an ecosystem component, is well studied and perhaps understood better for the wolf than any other carnivore. As such, it is surprising that little work has been done to assess the impacts of wolf predation on the population dynamics of beaver, an important alternate prey in many ecosystems. Here we used long-term data to explore the spatial and temporal aspects of wolf and beaver ecology at Isle Royale to assess top-down, bottom-up and abiotic influences on the population dynamics of beaver. Our results indicated that at varying time-scales, wolf predation is an important top-down process. Over a multi-decadal period wolf predation serves as a destabilizing force and apparent competition with moose could lead to continued downward trends without a perturbation (e.g. large-scale disturbance). Over time scales that are short, 5-6 years, predation can be a stabilizing force reducing the population. We were unable to implicate data on precipitation and stream flow as representatives for water availability (abiotic), a requisite for beaver dispersal, as an important abiotic influence in beaver population dynamics. Additionally, we demonstrated the importance of beaver as a

bottom-up influence for wolves during a period of high wolf abundance and low moose to wolf ratios.

The influence of predation on beaver population dynamics has been heretofore relatively overlooked. We demonstrated the importance of predation for beaver whose population dynamics have traditionally been thought be controlled from bottom-up, long-term dynamics. Equally important, the incorporation of the appropriate time scale is critical for evaluating how top-down, bottom-up and abiotic processes influence population dynamics.

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Appendix A.

Historical narrative of beaver research on Isle Royale National Park, Michigan, USA.

Scientific investigations of beaver at Isle Royale National Park began with observations. Beaver were first observed by John Tanner around 1790 (James 1830) and were notably absent with the exception of a few old lodges mentioned during a land survey in 1847 (Ives 1847). This absence continued through the 19th century (Adams 1909) as beaver were likely extirpated (Shelton 1966), or were purposefully not mentioned because their pelts were valuable, equivalent to \$875 in today's US currency (Romanski and Belant 2008).

The first scientist to discuss beaver was Adolph Murie, who described 27 locations in which he observed beaver sign in 1929 and 1930. Analysis of 1930 aerial photography identified a portion of those locations identified by Murie and an additional 27 sites (Shelton 1966). With additional extrapolation using results from his study, area and proportion of active vs. non-active sites, Shelton estimated that approximately 146 sites were on Isle Royale at this time and that 103 were active. Murie felt that beaver would have been abundant were it not for the activities of poachers. By the mid 1940s beaver became quite abundant.

The first aerial survey occurred on October 15th, 1945 and discovered a “good many worked out” colonies whose status was attributed to local resource depletion (Gilbert 1946). The first intensive study of beavers on Isle Royale was by Robert H.

Gensch of the U.S. Fish and Wildlife Service in May and June of 1946 (Gensch 1946) and was followed by Krefting and Lee (1948), of the same agency. These studies were assessing food reserves. Later, Krefting (1963), using the Gensch 1945 aerial survey and his own observations made during several years of moose browse studies on the island offered some information on the beaver population. He estimated that during the period 1945-1950, 150-200 active colonies occurred on the island. Using Bradt's (1947) figure of 4.0 beaver per colony with only one lodge, which Krefting felt was most often the case on Isle Royale, he estimated the population to be 600 to 800 animals, or 3 or 4 per square mile. Shelton profited that this estimate was conservative

Shelton's PhD dissertation (1966), the seminal work for beaver ecology on Isle Royale National Park, determined the status of beaver and their environmental relationships via live-trapping, intensive note taking and aerial survey between 1960 and 1963. Using information from Murie and Gilbert, Shelton estimated the population at 500 to 600 animals in 1930, and between 1000 and 1300 in the late 1940s. The population declined hereafter, likely caused by epizootic tularemia, widespread in the Great Lakes region at that time. Live-trapping at 31 sites provided an average of 6.4 beavers per colony and when combined with 140 active colonies determined by aerial survey and ground reconnaissance Shelton estimated a total population of 900 animals. Growth rates and weights were comparable to other populations. Kits comprised 40% of the summer population and juvenile mortality was low until the third year, when dispersal increased vulnerability to gray wolf (*Canis lupus*) predation. Beavers began to deplete their favored food, quaking aspen (*Populus tremuloides*). As available aspen decreased,

beavers ate more paper birch (*Betula papyrifera*), shrubs and aquatic plants. Around 15 % of wolf scats collected contained beaver remains; however, this mortality did not overcome beaver productivity.

Shelton continued aerial survey for active beaver sign continued and partial counts were conducted in 1969 and 1973 and a full survey was completed in 1974. Thereafter, a complete survey was conducted biennially starting in 1978. Through 2004, only two observers were responsible for completing the survey, Phillip Shelton and Douglas Smith. During this time, Smith and Shelton (2002) documented two population cycles beginning with 125 active sites in 1962, increasing to 286 in 1974, then decreasing to 83 in 1980, followed by an increase to 204 in 1986 and gradual decline to about 50 sites in 2004. Smith and Shelton conducted double-counts in 1990 and 2002 in a DeHavilland Beaver. They estimated their sightability at approximately 0.96, in other words they estimated that they surveyed 96% of the total population.

Shelton and Peterson (1983) contemplated the wolf crash of 50 to 12 (later determined to be caused by an outbreak of canine parvo virus) and its relationship to the population dynamics of moose and beaver suggesting moose vulnerability and high beaver numbers led to increased number of wolves and ultimately the increased use of beaver between 1974-1980. They also comment on the lack of available forage for beaver the potential for increase predation risk while foraging. This lack of available forage and competition with moose, the authors suggest, could prevent the beaver population from reaching high numbers previously observed.

Moen et al. (1990) studied the cumulative effects of moose and beaver herbivory in a selected portion of northeastern Isle Royale. Using the analysis of aerial photography, their results showed that beaver significantly reduced aspen overstory from 140 stems per hectare to 27 between 1957 and 1978. Balsam fir was more prevalent in beaver cut areas as opposed to non-cut areas. Moose herbivory combined with the beaver changes were suspected to alter succession and change soil fertility.

A renewed aerial survey effort during 2006-2008, using intensive coverage in a double-count of the entire island, Rolf Peterson and Mark Romanski revealed many more active beaver sites than the previous counts. From three surveys in 2006-2008 a stable population was inferred, but one with considerable annual turnover. Results of a fourth consecutive annual survey in 2009 confirmed the approximate number of active beaver colonies determined in 2006-2008, but also indicated that a real decline in beaver had occurred by 2009, in line with the long-term decline in beaver revealed by surveys prior to and including 2004 (Peterson and Romanski 2009).

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