

May 3, 2000

Algonquin Wolf Advisory Committee Member,

This letter introduces a report prepared by Drs. John A. Vucetich and Paul C. Paquet on the demographic viability of the population of wolves in Algonquin Provincial Park. The report is a response to a request from some members of the Algonquin Wolf Advisory Committee for an independent assessment of the wolf population data collected by Dr. John Theberge. This report is also a response to an explicit recommendation from the Population & Habitat Viability Assessment Workshop (Minden, Ontario, 15-18 February 2000). This request is explicated on page 6 of the draft report that was produced by participants of that meeting.

We hope that the Algonquin Wolf Advisory Committee finds this report useful. If you have any concerns or questions regarding the information, analyses, interpretations, or conclusions of this report please do not hesitate to contact either J. Vucetich or P. Paquet. Our contact information is included on the cover sheet of this report.

Sincerely,

John Vucetich

Paul Paquet

THE DEMOGRAPHIC POPULATION VIABILITY OF ALGONQUIN WOLVES

Prepared for:
The Algonquin Wolf Advisory Committee
May, 2000

In response to:
a request from several members of
the Algonquin Wolf Advisory Committee
&
an explicit recommendation from the
Population & Habitat Viability Assessment Workshop
(Minden, Ontario, 15-18 February 2000)

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Table of Contents

I. Purpose	3
II. Some criteria for population viability	3
III. The quality and quantity of data and the limitations of this assessment	4
IV. Dealing with uncertainty	4
V. Assessing population decline with trend data	5
<i>The data</i>	
<i>The analysis</i>	
VI. Assessing population viability with recruitment and mortality data	8
VII. Assessing population viability by examining fluctuations in population size	12
<i>Background</i>	
<i>Analysis</i>	
VIII. Assessing population viability by examining ecological and behavioral functions....	13
<i>Wolf-prey relationships</i>	
<i>Trends in pack size</i>	
<i>Rate of den site re-use</i>	
<i>Rates of territory vacancy</i>	
<i>Conclusion</i>	
IX. Causes of mortality	16
X. Summary	17
References	18
APPENDIX: A QUALITATIVE ANALYSIS OF THE VALUE OF FULLY PROTECTING ALGONQUIN WOLVES	19

I. Purpose

This document provides an assessment of viability for a population of wolves residing primarily in the eastern portion of Algonquin Provincial Park, Ontario. Population data were collected by John and Mary Theberge (University of Waterloo) between 1988 and 1999. This document responds to a request from the Population Demography Working Group, which was formed during a meeting charged with conducting a Population Viability and Habitat Assessment (PHVA) of wolves in and around Algonquin Provincial Park (please refer to page 6 of the draft report from that meeting). The meeting was held from February 15th to 18th, 2000 and was facilitated by the Conservation Breeding Specialist Group (CBSG, a division of the World Conservation Union, IUCN).

Our analysis consists primarily of a quantitative analysis of several aspects of the demography of Algonquin wolves. To provide a complete assessment, we also include some discussion of our findings as they relate to considerations for fully protecting the Algonquin wolf population. In an appendix (pg 19), we also include a qualitative assessment of the value of fully protecting the Algonquin wolf population. This qualitative assessment is based on our personal knowledge of and experience with the challenges of effective carnivore conservation.

II. Some criteria for population viability

Population viability is a multifaceted concept, and a population may be inviable for one or many reasons. This document considers several important (but not all) criteria for assessing the viability of the Algonquin wolf population:

- A. A viable population must not exhibit chronic decline in population size.

- B. A viable population must exhibit a low risk of local extinction over a long period (e.g., 100 years). Thus, surrounding unprotected populations of wolves should not be expected to prevent the local extinction of a park population.

- C. A viable population should exhibit average recruitment rates that exceed average mortality rates.

- D. A viable population must be able to perform, unimpaired, all of its ecological functions and exhibit behavioral characteristics typical of a healthy population. That is, mere existence of a population does not constitute viability.

Our analysis also recognizes that the abundance of prey constrains the viability of a wolf population. Viability can be precluded if prey are not sufficiently abundant. Even if prey are sufficiently abundant to support a viable population, prey abundance constrains the (maximum and minimum) number of wolves that would constitute an ecologically healthy and sustainable system (see *Wolf-prey relationships*).

III. The quality and quantity of data and the limitations of this assessment

Despite clearly delineated criteria, assessing population viability is notoriously difficult. Most often, assessments of population viability are based on data of meager quality and quantity. In contrast, the Population Demography Working Group agreed unanimously that data from the study population in Algonquin are extensive and of the highest quality possible (please refer to the final report produced by that meeting for details). These data (collected from 1988 to 1999) represent the longest continuous study of wolves in Canada, and one of the longest studies of wolves in the world.

Despite the excellent quality of these long-term data, scientific methods are still unable to provide definitive answers to some questions, even some simple questions. For example, scientific methods are unlikely to allow us to conclude definitively that either “Yes, the population is declining” or “No, the population is not declining.” The best any analysis can do is assess the *probability* that the population has experienced a significant decline over the past 11 years. Such limitations arise from inherent uncertainties in the behavior of natural systems and cannot be avoided or circumvented.

The analyses described in this document are based on data collected from wolves and wolf packs that reside primarily in the east half of Algonquin Provincial Park. The conclusions reported in this document refer explicitly to the study population. Therefore, conclusions about the viability of the entire park population can be made only by means of educated inferences about how the study population may or may not differ from the rest of the park population.

Despite these limitations and uncertainties, speculation about the causes of a potential decline is possible and essential for development of management plans aimed at halting and reversing unnatural or undesirable declines. In this analysis, we assess the plausibility of several potential causes of decline (e.g., excessive mortality rates, excessive human-caused mortality, declining prey biomass, disease).

IV. Dealing with uncertainty

Given the inherent variability of many natural populations and the limited amount of data that are often available from a population, the best available methods for detecting population

decline and loss of viability have limited sensitivity. That is, population declines and losses of viability are often substantial (or have been occurring for a long time) before we detect them. In fact, important declines in population or losses of viability can occur without being easily detected.

In situations like this when levels of uncertainty are high, an a priori decision about where the burden of proof should lie is critical. For example, should we assume a population is viable (i.e., now and in the future) until shown otherwise? Conversely, if current evidence provides some reasonable suggestion that the population is threatened, should we continue to assume the population is inviable until evidence clearly demonstrates that the population is not inviable? The precautionary principle should guide resolution of these issues. That is, one should compare the likelihood and consequences of: 1) deciding that the population is viable when it may in fact not be, and 2) deciding that the population is inviable when in fact it may be. For example, if one decided that the population was viable, could the consequences of actions (or non-actions) associated with that decision be easily reversed should it later be discovered that the population is not viable? Alternatively, if one decided that the population was inviable, could the consequences of actions (or non-actions) associated with that decision be easily reversed should it later be discovered that the population is viable?

V. Assessing population decline with trend data

The data. — The primary evidence for assessing whether or not the Algonquin Park wolf population is declining is annual estimates of population density (number of wolves per 100 km²) from 1988 to 1999 for a study population on the east side of the park. The area typically inhabited by the study population constitutes approximately ½ of the total area of Algonquin provincial park (i.e., ~2700 km²). Each annual estimate was obtained by standard aerial survey techniques commonly employed to estimate wolf density. To facilitate aerial surveys, at least one wolf in each pack of the study population was fitted with a radio collar. Between 1988 and 1999, the number of study packs varied from 5 to 11 (median = 8). Radio collared wolves were used to locate packs during each flight. Flights were repeated as often as possible throughout the winter, and pack size was estimated by visually counting wolves from the plane. Estimated pack size was the maximum number of wolves seen at one time. Population density is the sum of all pack sizes divided by the sum of all the pack territories. Pack territories were based on minimum convex polygons. This calculation of density differs slightly from that presented by John Theberge in *The Wolves of Algonquin Park: PHVA Briefing Book*. In this document, J. Theberge calculates the denominator of each density estimate as the sum of territory sizes plus small interstitial areas between packs. Because we cannot estimate interstitial areas around each pack

equally for all packs over time, we omitted these areas. This approach overestimates absolute density, but is required to reduce the potential for biased estimation of population trend.

Aerial surveys may not detect all lone wolves and pack members, but are the best possible method for surveying wolf populations. Despite missing some wolves, this method is unlikely to bias attempts to assess population decline. That is, these surveys may slightly underestimate the *number* of wolves, but are unlikely to over- or underestimate *trends* in size over time.

The denominator of these density estimates (i.e., sum of territory sizes) also varies annually. This variation is not ideal from a statistical standpoint. However, we are unaware of more effective ways to estimate wolf abundance. We are also unaware of better ways to analyze the existing data. However, reasons for concern over this issue may be limited, because the total area (i.e., measured in km²) did not vary systematically during the study period ($p = 0.23$, simple linear regression of total area on year). Thus, we have no reason to suspect that the data provide a biased impression by either over- or underestimate *trends* in size over time. If a decline (or increase) were present, this additional annual variation in size of the study area could obscure increasing or decreasing trends. Thus, if a trend is detected, it is doubtful that the hypothesized trend is an artifact of annual variation in size of the study area. Alternatively, if no trend is detected, it may exist but be obscured by this variation.

The analysis. — To assess whether the population is declining we employed a method used to assess the viability of numerous endangered species and small populations including the whooping crane, California condor, Yellowstone grizzly bear and many others (Dennis et al. 1991). The method is based on a simple, yet robust, mathematical expression of population dynamics:

$$N_{t+1} = N_t R_t, \quad (1)$$

where N_t is the population size or density in year t and R_t is the annual finite rate of population increase. If R_t is, on average, greater than one, the population grows; and, if R_t is, on average,

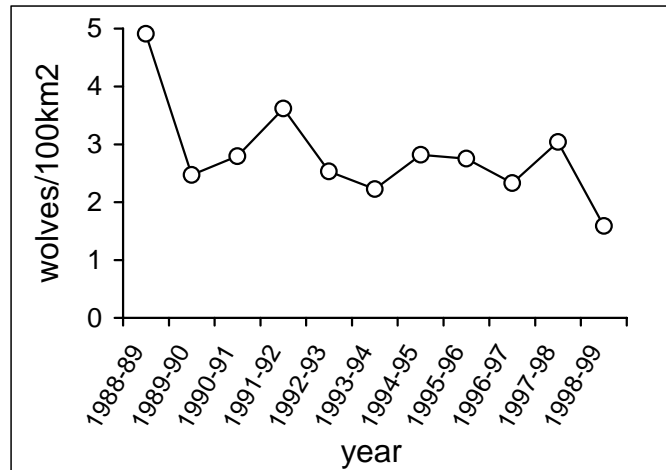


Fig. 1. Population density of the Algonquin study population from 1988 to 1999.

less than one the population declines. Because the statistical properties of R_t are complex, it is difficult to assess whether R_t tends to be greater than or less than one. (This statistical complexity is also the reason that assessing population decline by regressing population density on time is inappropriate. Simple linear regression requires the response variable [i.e., population size or density] to be normally distributed. Generally, population size is not normally distributed.) The acceptable approach for avoiding these statistical difficulties is to consider the log-transformed population dynamics. Therefore, let the natural logarithm of N_t (i.e., $\ln[N_t]$) be denoted as n_t . By following the algebraic rules for manipulating logarithms, the dynamics of equation (1) are equivalently expressed as:

$$n_{t+1} = n_t + r_t, \tag{2}$$

where r_t is the log-transformed growth rate. If the average value of r_t (denoted μ) is positive, the population grows; otherwise, the population declines. (Note: Under some circumstances population decline is expected for small positive values of μ . See *Assessing population viability by examining fluctuations in population size*. Otherwise, we can ignore this detail for this assessment). Extensive theoretical considerations and empirical evidence suggest that r_t and μ are normally distributed. Thus, assessing the probability that μ is positive or negative is straightforward.

Our first step is to derive a series of r_t from the 11-year series of population estimates (Table 1). Algebraic manipulation of equation (2) indicates that each value of r_t is calculated as $n_{t+1} - n_t$. Next, we estimate μ by calculating the arithmetic mean of the series of r_t . The *estimated* value of μ is -0.113. Then, we estimate the variance of r_t (denoted σ^2) by calculating the unbiased sample variance of the series of r_t . The *estimated* value of σ^2 is 0.128. Thus, the estimate of μ follows a normal distribution with mean value of -0.113 and a variance of 0.128/10, where 10 is the length of the time series of r_t . Moreover, the probability that the true value of μ is negative is equal to the portion of this estimated normal distribution that is less than zero. From this analysis, we

Table 1. Annual estimates of population density and log-transformed growth rates.

Year	N_t	$n_t = \ln[N_t]$	$r_t = n_{t+1} - n_t$
1988-89	4.91	1.59	
1989-90	2.47	0.91	-0.69
1990-91	2.80	1.03	0.12
1991-92	3.62	1.29	0.26
1992-93	2.53	0.93	-0.36
1993-94	2.23	0.80	-0.13
1994-95	2.82	1.04	0.24
1995-96	2.75	1.01	-0.02
1996-97	2.33	0.85	-0.17
1997-98	3.04	1.11	0.27
1998-99	1.59	0.46	-0.65

conclude there is an 84% chance that μ , the average log-transformed growth rate, is less than zero, and that the Algonquin study population has been declining.

Besides assessing the probability of decline it is useful to assess the probability that the population is exhibiting a biologically important decline. Although quantifying what is an important decline is subjective. Most (if not all) population biologists would agree that a population with an average annual change in population size of ≤ -0.05 would be at great risk of extinction. This analysis predicts a 71% chance that the population has been characterized by an average annual change in population size of ≤ -0.05 (i.e., the rate of decline exceeds 5% per year).

Given the high probability of population decline, we highlight some criteria that may and may not be appropriate for future assessments of population recovery. Any framework for such assessment should recognize both the population's average growth rate *and* abundance. For example, if the future trajectory of the population suggests that the population does not have a negative growth rate, one could conclude that the population has stopped declining. However, this condition alone is insufficient to conclude that the population has recovered and is no longer threatened. Future assessments should *also* consider whether average wolf abundance is within an acceptable range. Such a range could, for example, be defined by the average abundance of wolves before the population decline.

VI. Assessing population viability with recruitment and mortality data

This analysis focuses on assessing the probability that average annual recruitment is less than average annual mortality. We estimated annual mortality as the proportion of radio-collared animals that died each year from 1988 to 1999. Annual estimates of mortality rate are given in Figure 2 (column *h* of Table 2 also reports the survival rate which equals one minus mortality rate). Information about annual recruitment was obtained while examining wolves fitted with radio-collars. Each radio-collared wolf was aged based on tooth size. Annual recruitment rate was estimated as the proportion of examined wolves that were recruits. Because this method does not distinguish between yearling and two-year-old wolves, the calculated proportion represents a “two-cohort” recruitment rate. (For additional details on the estimation of recruitment and mortality see *CBSG Wolves of Algonquin Park PHVA Briefing*, pp.150, 158.)

To compare mortality and recruitment rates properly, we must remove the two-year-old component of the recruitment rate. To do this, we used the following recursive algorithm (The mechanics of this algorithm are demonstrated in Table 2 which is at the end of this section):

- 1) The *number* of yearling and two-year-old wolves in year t is the product of the estimated population size in year t (= population density \times study area) and the “the two-cohort

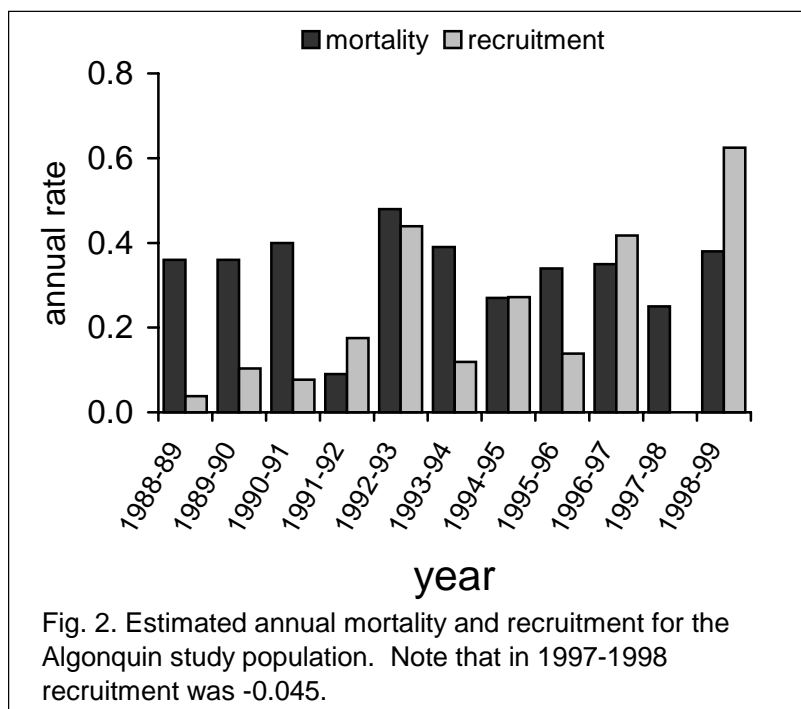
recruitment rate” for year t .

- 2) The *number* of two-year-old wolves in year t is the number of yearlings in year $t-1$ times the annual survival rate of yearlings in year $t-1$. The annual survival rate is obtained from the proportion of radio-collared wolves that survive each year.
- 3) The *number* of yearlings in year t is the difference between (1) and (2).
- 4) The yearling recruitment rate in year t is the result of (3) divided by the estimated population size.

In this algorithm, we multiply (in step 1) *and* divide (in step 4) by the estimated population size. Thus, estimated population size needs only to reflect relative abundances over time, and not exact population size. This algorithm also depends on an estimate for the proportion of yearling recruits in the first year of the data set (i.e., 1988). Although we have little basis for determining this value, annual recruitment estimates are insensitive to this initial value. Average annual recruitment of yearlings ranged from 0.213 to 0.215 as the initial proportion of yearlings varied from 0.1 to 0.9. For the remainder of our analysis, we assumed that the initial proportion of yearlings was 0.5 which yielded an average annual recruitment rate of 0.214 (compared with an average annual mortality rate of ~ 0.33). A signed-rank test shows that the median annual mortality rate exceeds the median annual recruitment rate (one sided p-value = 0.045). Two possible explanations account

for negative recruitment in 1997-98. The negative value could be the result of sampling error. However, the negative value could also have arisen because recruitment represents birth, immigration and emmigration. Thus, a negative value would indicate a year in which emmigration exceeded immigration and births. If this were the case (and it may be), the population would be acting (at least in some years) as a source of wolves to surrounding populations. If

true, this would be unusual, because the population would be both declining and providing



wolves to surrounding populations. Thus, despite this population's decline, surrounding populations could be even less viable. Notwithstanding these uncertainties, our analysis shows that mortality tends to be higher than recruitment – a condition leading to population inviability.

The imbalance between mortality and recruitment suggests the Algonquin population is characterized by: 1) elevated mortality, 2) depressed recruitment (or natality), or 3) both elevated mortality *and* depressed recruitment. The imbalance between recruitment and mortality could result from any one (or combination of) the following factors: declining prey biomass, unsustainable levels of human-caused mortality, and disease (This list is not meant to be exhaustive. Please see *Causes of mortality* for additional information).

Regardless of whether mortality is elevated and no matter its potential cause, an especially puzzling aspect of this population's demography is the population's either low recruitment or lack of compensatory recruitment. Several unprotected populations exposed to intense human harvest exhibit rates of mortality of ~30% (e.g., Fuller 1989 and references therein). Some (but not all) of these populations also appear to have exhibited elevated levels of compensatory recruitment, such that average annual rates of population increase were positive. In contrast, the Algonquin population exhibits unexplainably low levels of recruitment. Low recruitment could be a consequence of this population being situated on the periphery of the geographic range of this species (Regardless of our current uncertainty about the taxonomy of Algonquin wolves, they would be near the periphery of their geographic range). One related process (but not the only process) that *could* lead to depressed recruitment is that: 1) high mortality creates territory vacancies filled by canids from surrounding areas (please see *Rates of territory vacancy* for details), 2) these vacancies are filled by coyotes that hybridize with wolves (please see page 174-187 of the *CBSG Wolves of Algonquin Park PHVA Briefing* for details) and 3) coyote-wolf hybrids may exhibit reduced fecundity in some natural environments such as Algonquin Provincial Park. (No studies have been conducted to assess the viability of wolf-coyote hybrids in the wild.)

Populations on the periphery of a geographic range may be more vulnerable to exhibiting low recruitment for a variety of other reasons (Lesica and Allendorf 1995; see also Lomolino and Channell 1995; Curnutt et al. 1996). Because of their vulnerability, and because range reduction of a species begins with the loss of peripheral populations, ecologists have long recognized the conservation of populations near the edge of their geographic range as a critical component of large-scale conservation.

Table 2. The algorithm used to remove two-year-old wolves from the estimates of annual recruitment. The bold-faced number is based on the arbitrary assumption that 50% of the “recruits” handled in 1988 (column g) are yearlings. The predicted annual recruitment rate is insensitive to this initial value. See text for details.

a	b	c	d	e	f	g	h	i	j
Year	wolves/ 100km²	population size (= b × 27)	total number of wolves handled	number of yearlings and two-year-old wolves handled	“two- cohort” recruitment rate (= e ÷ d)	number of yearlings and two year old wolves in population (= f × c)	annual survival	number of yearlings in the population (= g_t - [i_{t-1} × h_{t-1}])	yearling recruitment rate (= i ÷ c)
1988	4.91	133	13	1	0.08	10.20	0.64	5.10	0.04
1989	2.47	67	13	2	0.15	10.27	0.64	6.93	0.10
1990	2.80	75	11	3	0.27	20.59	0.60	5.83	0.08
1991	3.62	98	15	7	0.47	45.58	0.91	17.09	0.17
1992	2.53	68	15	5	0.33	22.78	0.52	30.03	0.44
1993	2.23	60	12	5	0.42	25.04	0.61	7.16	0.12
1994	2.82	76	15	5	0.33	25.37	0.73	20.67	0.27
1995	2.75	74	18	8	0.44	33.03	0.66	10.29	0.14
1996	2.33	63	10	2	0.20	12.58	0.65	26.24	0.42
1997	3.04	82	14	4	0.29	23.44	0.75	-4.48	-0.05
1998	1.59	43	8	3	0.38	16.10	0.62	26.80	0.62

VII. Assessing population viability by examining fluctuations in population size

Background. — An important, but often overlooked, component of population viability is annual fluctuation in population size (FPS). For example, it is possible for an isolated population with a positive average growth to exhibit high levels of extinction risk, if FPS is too great. Any complete assessment of population viability must consider the influence of FPS.

Analysis. — We begin this analysis by assuming that the study population is isolated from other wolf populations. Although technically incorrect, an analysis based on this assumption reveals what could happen if the study population became isolated. Presumably, if the population were viable, it should have reasonably low extinction risk even if isolated from other populations. Within this context, we can examine the influence of FPS on extinction risk in Algonquin wolves with the population model represented by equation (2): $n_{t+1} = n_t + r_t$, where r_t is properly modeled as a normally distributed random variable with mean μ and variance σ^2 . If maximum population density or carrying capacity (K) and current population size (N_o) are specified, the mean time to extinction (*MTE*) can be predicted according to Equation 8 of Foley (1994:126).

We use this equation to explore the effect of FPS on the *MTE* of an isolated population with demographic parameters comparable to that of the study population. In this model, FPS is characterized by σ^2 . As σ^2 increases, so does FPS. Previously (see *Assessing population decline with trend data*), we estimated μ to be -0.113 and σ^2 to be 0.128. Based on the observed maximum population density since 1988, we estimate K to be 5.0 wolves/100 km². (The accurate estimation of K is routinely difficult. Although many models base the estimation of K on the maximum observed population size, such values may over- or underestimate the true value of K . In fact, our estimate of K is likely to overestimate the true value. Here the model results will be relatively insensitive to the value of K , because the growth rate is a relatively large negative value.) We also used the most recent population density estimate from the study population (1.59 wolves/100 km² in 1999) as an estimate of N_o .

Figure 3 details the results of our calculations that highlight the importance of FPS in the viability of the study population. As the average growth increases (moving from left to right along the x -axis), the mean time to extinction increases. Specifically, the model predicts that the *MTE* would increase by a factor of 2.6 if the average growth rate increased from -0.113 (its current predicted value) to zero. Thus, the model demonstrates that increasing the average growth rate can increase the viability on the population. However, of comparable importance is FPS. For example, if the estimated level of FPS (i.e., $\sigma^2 = 0.128$) were decreased by 50% the *MTE* is predicted to increase by a factor of 2 (when the average growth rate is zero). Alternatively, if the estimated level of FPS were increased by 50% the *MTE* is predicted to decrease by a 67% (when the average growth rate is zero).

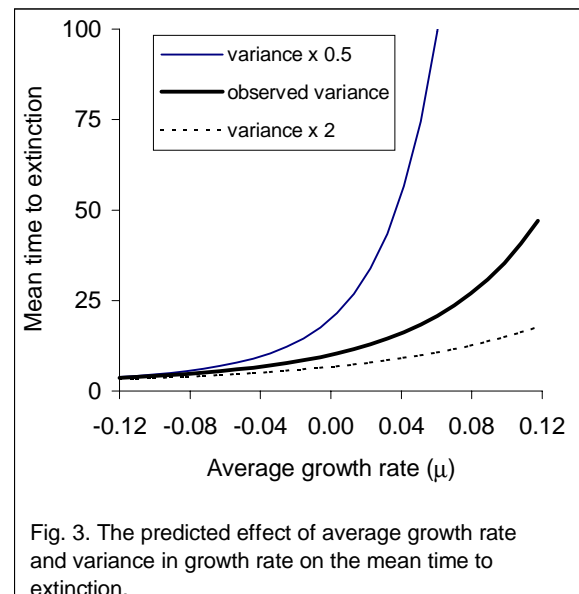
It is critical to recognize that the results of Figure 3 are best interpreted qualitatively (e.g., increasing σ^2 leads to a decrease in *MTE*). Without expert knowledge of population biology, it may be misleading to focus on the quantitative results presented in Figure 3 (e.g., the mean time to extinction is 20 years when $\mu = 0$ and $\sigma^2 = 0.06$). Thus, the critical messages of this analysis are: 1) fluctuations in population size may be sufficiently large to make the Algonquin wolf population inviable, and 2) a reduction in population fluctuations could be an important for increasing the viability of the population.

These results highlight the value of considering if and how FPS can be reduced through management action. Because little is known about the population biology of wolves, general principles of population biology will provide the best motivation for understanding how potential management action could reduce FPS. The variance in growth rate (one measure of FPS) is roughly the sum of the variances of the processes that constitute the growth rate (minus a covariance component that may be demonstrated to be relatively small). For example, because the growth rate is the difference between mortality and recruitment, the variance in growth rate is approximately the sum of the variances of recruitment and mortality. Similarly, the variance of mortality is the sum of the variances of the components of mortality. Specifically, the variance of mortality is approximately the sum of the variance in human-caused mortality and natural-caused mortality. Therefore, a reasonable (but untested) hypothesis is that a reduction in human-caused mortality would reduce the variance of mortality and the variance in growth rate, and thus reduce FPS and increase population viability.

VIII. Assessing population viability by examining ecological and behavioral functions

The existence of a population is not, by itself, an adequate criterion for population viability. In addition, a population must be sufficiently abundant and protected (from anthropogenic influences) to be able to perform its ecological functions and exhibit normal behavior. In each of the following sections, we review some of what is known about the study population's functioning in the ecosystem.

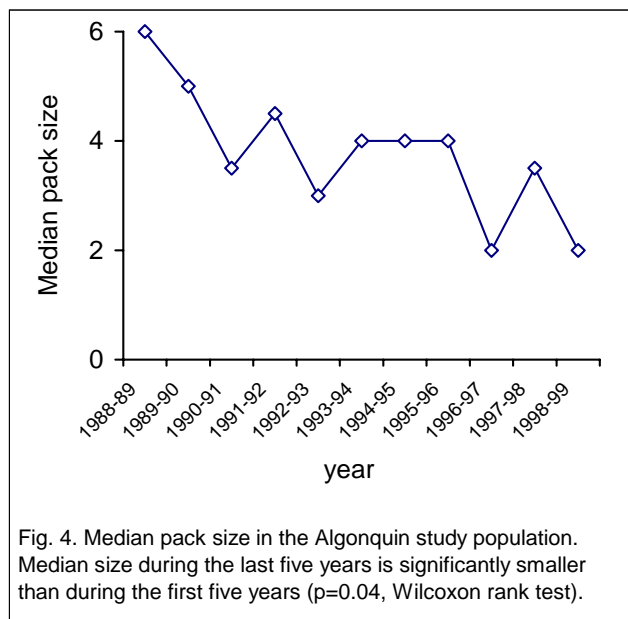
Wolf-prey relationships. — Throughout most of North America wolves prey primarily on



ungulate species. Empirical studies reveal a predictable relationship between ungulate density and wolf density (Keith 1983, Fuller 1989). Based on this empirical relationship, the density of wolves in Algonquin appears, at least superficially, to be appropriate given the estimated density of moose and deer. However, Algonquin wolves prey on beavers more than do most other North American wolf populations. Approximately 1/3 of the diet is beaver. It is unclear whether this elevated use of beaver is due to high beaver abundance, greater preference for beaver, or a combination of both. Because beaver are a large portion of the diet, evaluating “normal” wolf abundance based solely on ungulate density may be inappropriate. Perhaps Algonquin wolves should be more abundant than predicted by ungulate biomass. Accordingly, we are uncertain what constitutes “normal” wolf density given the availability of prey.

Aside from the observation that wolf density may be within the range predicted by ungulate biomass is the issue of whether the decline in wolf abundance between 1988 and 1999 is the result of a population decline in prey during the same period. Indices of ungulate abundance (see page 167-168 of the *CBSG Wolves of Algonquin Park PHVA Briefing*) do not show that ungulate abundance has declined since 1988. Thus, the available evidence does not suggest that the decline in wolf abundance can be attributed to a decline in prey abundance. (*The role of human caused mortality* provides additional support for this conclusion.)

Trends in pack size. — Median pack size appears to have declined during the past 11 years of study (Fig. 4). A Wilcoxon rank test also indicates that median pack size is significantly lower during the last five years of study than during the first five years of study ($p=0.04$). The decline in pack size is probably related to the decline in population size. However, because pack size is a major determinant of per capita rates of predation (Thurber and Peterson 1993), it is an important factor relating to the ecological functioning of a wolf population. Human-induced changes in pack size will lead to anthropogenically-induced changes in predation. Because the most valuable role of a park is as a benchmark for healthy ecosystem functioning, it is critical that predation,



one of the fundamental functions of a wolf population, is left as undisturbed by human activity as possible. Altering pack size undoubtedly alters the nature of predation in a wolf population.

Rate of den site re-use. — Den site quality is an important component of wolf fitness. A poorly selected den site may be associated with low reproductive success (Mech et al. 1998). High rates of den site re-use may result from information sharing of high quality den sites among generations of wolves, and may be typical for unimpaired wolf populations (Mech 1970). For example, in Isle Royale National Park the rate of den site re-use probably exceeds 75% (R. Peterson, *pers. comm.*). In contrast, the rate of den site re-use for the study population in Algonquin was 13% (J. Theberge, *pers. comm.*). This low rate of re-use likely reflects high rates of turnover among pack members and consequent independent selection of den sites from year-to-year. Although measuring the fitness consequences of this apparently impaired behavior is difficult, a viable wolf population is unlikely characterized by such a low rate of den re-use.

Rates of territory vacancy. — In most studied wolf populations, wolf territories are only rarely left vacant. If a wolf pack is eliminated in a single year, the territory is typically refilled in less than a year (e.g., Peterson and Page 1988, Peterson et al. 1998, Mech et al. 1998). In the Algonquin study population 12 territory vacancies were observed between 1988 and 1998. This corresponds to an 11% rate of pack vacancy (i.e., 12 vacancies divided by the total number of “territory years” during the period of observation). Pack vacancy occurs when wolves from surrounding areas fail to “recolonize” the vacant territory. Low rates of recolonization may be symptomatic of low wolf population densities (or the low annual production of surplus wolves) in areas surrounding the study population. We might expect this situation for a wolf population suffering habitat alienation due to human disturbance, or any population that is located near the edge of its geographic distribution.

These observations highlight the special importance of conserving populations near the edge of their geographic range. Large-scale considerations are essential for the conservation of any species, and the conservation of populations along the edge of a geographic range is critical for the large-scale conservation of a species.

Conclusion. — The previous four sections reveal some clear ecological patterns and population trends (e.g., Fig 4). However, the limited scope of these sections reflects our lack of knowledge regarding the functioning and behavior of wolf populations. This gross ignorance prevents a comprehensive assessment of the Algonquin situation and increases the uncertainty of our interpretation and that of others. Consequently, management of this population should be very

conservative (precautionary principle). This ignorance highlights the appropriateness of full protection and continued monitoring of this population. Continued monitoring should *not* be used as a tool to determine if full protection achieves some specified management goal. Rather, continued monitoring is required to reduce our ignorance about how a healthy, protected population functions and behaves. This information is essential for judging the health of other unprotected populations.

Similar views regarding the critical importance of protected areas as ecological baselines are common among ecologists (e.g., Schonewald-Cox 1988, Janzen 1983; see also Woodroffe and Ginsberg 1998). One recent review of the subject argued that:

Modern man is affecting nearly every biome on earth. There is a growing urgency to monitor such effects on the functioning of ecosystems, and monitoring requires baseline data from areas where modern human impacts have been kept to a minimum. Humans have set aside parks and protected areas for various reasons throughout their history. Irrespective of their historical origins and in absence of suitably large alternative areas, protected areas have become baselines for measuring ecological change...

Ecological baseline areas must necessarily be large enough to represent natural habitats and natural ecosystem dynamics. It is unlikely that any area is now completely free of human impacts, but baselines must be relatively free of direct impact present and in the future... This function for parks [i.e., serving as a baseline] is so urgent that it supersedes any other historical roles that these areas may have had... The larger the baseline area the more likely it will represent relatively undisturbed processes; national parks [and similar protected areas] should be expanded as much as possible to meet this requirement. — A. R. E. Sinclair 1998:399-400

IX. The role of human caused mortality

The information provided on pages 198-214 in *The Wolves of Algonquin Park: PHVA Briefing Book* provides a reasonable summary of the causes of mortality. Nevertheless, we reinforce several conclusions that appear in that document:

- 1) Mortality does not appear to be related to food stress. If mortality were related to food stress, one would expect that significant wolf mortality would be due to malnourishment, starvation, inter- and intraspecific strife resulting in deaths, and high rates of dispersal. None of these have been observed. This lack of evidence for food stress related mortality further suggests that wolf declining has not been due to a decline in prey (please see *Wolf-prey relationships* for additional support).
- 2) Approximately 2/3 of all mortality is human caused.
- 3) It is unreasonable to make inferences about the sustainable levels of harvest for today's population by considering that before 1958 annual harvested rates were about 18%. For this purpose, today's population is not comparable with the population before 1958.

- 4) Very little (if any) of the human-caused mortality appears to be compensatory.
- 5) Based on the assumption of an age-independent mortality rate of 35%, the median age of death for a wolf that survives to be a yearling is between 2 and 3 years old. In contrast, the median age of death for a yearling wolf from Isle Royale National Park (the only unharvested population for which detailed mortality data are available) is between 5-6 years old (calculated from Table 1 in Vucetich et al. 1997). Besides the direct negative consequences, shortened median life spans are likely to have synergistic effects that are negative. For example, shortened life spans could result in few breeding wolves gaining sufficient experience that may be required to increase recruitment rates significantly.
- 6) Insufficient time has passed and/or insufficient analysis has been conducted to assess whether seasonal protection of wolves in Hagarty, Richards, and Burns townships has affected mortality.
- 7) Field observations by J. Theberge provide no suggestion that disease, has been an important cause of mortality during the study period.

X. Summary

Our analysis indicates a high probability that the study population has been in decline during the past 11 years. Moreover, it is likely that the decline has been severe (i.e., 71% chance of declining an average annual decline of 5%). In addition, we have shown that annual mortality rates (~33%) typically exceed annual recruitment rates (~21%). We have also shown that high levels of variation in the annual growth rate threaten the population's viability.

The study population is characterized by wolves with shortened life spans, declining pack size, low rates of den site re-use, and high rates of territory vacancy. Although the complete influence of these factors on the population's viability is difficult to quantify, these patterns further support the urgency of increasing the protection currently offered to this population.

This analysis does not address viability concerns associated with the genetic constitution of Algonquin wolves nor does it address trends in the morphological characters of wolves within the population. However, these factors may be relevant to the population's viability.

Ungulate density does not appear to have declined since 1988. Thus, prey decline is not a suspected cause of the wolf population decline that has occurred since 1988. In contrast, human-caused mortality (which constitutes 2/3 of all mortality) may be the primary cause of population decline. Substantial reduction of human-caused mortality may be the only way to restore the viability of this population.

Additionally, the absence of critical baseline data on the ecosystem functioning and

behavior of fully protected wolf populations provides a sufficient reason to protect fully and continue monitoring the wolves of Algonquin Provincial Park. We believe the information resulting from such action is essential for judging the health of unprotected wolf populations.

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APPENDIX: A QUALITATIVE ANALYSIS OF THE VALUE OF FULLY PROTECTING ALGONQUIN WOLVES

Currently, the wolves of Algonquin Provincial Park are not fully protected, because many, if not most, wolves occasionally travel outside the anthropogenically determined boundaries of the park. Extending full protection to the wolves of Algonquin Provincial Park represents an unprecedented opportunity. A decision to afford full protection would be highly significant at local and regional levels as well as of global significance for the conservation of wolves and carnivores in general. To assist the committee in exploring this significance, we have constructed a table that represents a framework for assessing the significance of full protection (Table A1 on page 20). We encourage the Algonquin Wolf Advisory Committee to discuss, scrutinize, and further develop this framework as a means of assessing the high value associated with full protection of this population.

The table also provides insight on an additional matter: The taxonomic classification of Algonquin wolves is uncertain (for some details see the Briefing Book distributed at the PHVA work shop). This uncertainty may lead some to conclude that a decision about protecting the wolf population should be postponed until after the taxonomic uncertainties are completely assessed. However, Table A1 indicates that the value of full protection is high regardless of the taxonomic status that is eventually assigned to the wolves of Algonquin Provincial Park.

Table A1. A framework for assessing the significance of fully protecting the Algonquin wolf population. This framework highlights the local, regional, and global significance of full protection. This framework also highlights that taxonomic uncertainty about Algonquin wolves does not reduce the value of full protection.

Significance Item	Relevant spatial scale(s)			Potential taxonomic determinations for the wolves of Algonquin Provincial Park*			
	Local	Regional	Global	<i>Canis lupus lycaon</i>	<i>C. lycaon</i>	<i>C. latrans lycaon</i>	<i>C. lupus</i> <i>x</i> <i>C. latrans</i>
Unprecedented educational value (due to Toronto’s proximity) ¹	x			✓	✓	✓	✓
High aesthetic value (due to Toronto’s proximity) ¹	x			✓	✓	✓	✓
Uniqueness associated with absence of a fully protected wolf population anywhere in North America ²	x	x	x	✓	✓	✓	✓
Special conservation value due to population’s location on the periphery of its geographic range ³		x	x	✓	✓	✓	✓
Concern of unwanted hybridization ⁴	x	x		✓	✓		
High research value ⁵		x	x	✓	✓	✓	✓
Highly endangered ⁶	x	x	x		✓		
An opportunity to include local citizens (e.g., trappers and deer hunters) in scientific monitoring of the wolf population. ⁷	x	x	x	✓	✓	✓	✓

**Canis lupus lycaon* = wolves in and around Algonquin are designated as a subspecies of the gray wolf; *C. lycaon* = wolves in and around Algonquin are designated as a new species of wolf (i.e., eastern Canadian wolf); *C. latrans lycaon* = wolves in and around Algonquin are designated as a subspecies

TABLE A1, CONT'D

of coyote; *C. lupus* x *C. latrans* = wolves in and around Algonquin are considered to be primarily a wolf-coyote hybrid.

- ¹ For example, since the mid-1960's more than 100,000 people (many from the Toronto area) have participated in the wolf howling program of Algonquin Park. Perhaps more people have had this intimate form of contact with Algonquin wolves than with wolves from any other location in the world.
- ² With the exception of Isle Royale National Park, MI, possibly no other population of wolves in North America is fully protected. Also, see Haber (1996) for a related discussion.
- ³ For example, if the wolves of Algonquin are assigned as *Canis lupus lycaon*, then Algonquin is situated near the southern edge of this range. Alternatively, if the wolves of Algonquin are assigned as *C. latrans lycaon*, then Algonquin may be situated near the northern edge of this range. See Lesica and Allendorf (1995) and page 10 of this document for information on the value of populations situated at the edge of their geographic range.
- ⁴ Full protection may minimize levels of hybridization that are ultimately the result of shifts in the abundance of wolves and coyotes human alteration of the landscape.
- ⁵ The study of wolves in Algonquin Park is the longest study of wolves in Canada, and perhaps the second longest study in the world. The need to understand the dynamics of unharvested populations is critical and of global importance (Sinclair 1998).
- ⁶ If the wolves of Algonquin Park are assigned to be *Canis lycaon*, they will be members of a species whose total number of may not exceed a few thousand individuals – making them one of the most endangered canid species in the world. For context, approximately 5,000 African wild dogs remain in the wild (Creel and Creel 1998).
- ⁷ Full protection of Algonquin wolves could allow the Algonquin area to serve as an unprecedented model for the inclusion of local citizens in the effective conservation of natural resources. If Algonquin wolves were fully protected, local citizens could be employed to assist in monitoring the dynamics of Algonquin wolves. Such an arrangement could provide a source of income, and lead to an enriched culture as local citizens interact with scientists and develop new and more complete personal bonds with the local environment. Development of such a plan could be unprecedented in North America. With great success, North Americans have helped to develop similar programs in third-world countries (e.g., Lewis and Alpert 1997). However, examples of such successes in North America are rare and limited. In this way, full protection of Algonquin wolves not need be perceived

as an economic burden or a loss of cultural values for local citizens. If, however, Algonquin wolves were not protected, little motivation or incentive would exist to develop such ideas.