

From *The World of Wolves: New Perspectives on Ecology, Behaviour and Management*, edited by Marco Musiani, Luigi Boitani, and Paul C. Paquet. (Calgary: University of Calgary Press, 2010)

1.4 Will the Future of Wolves and Moose Always Differ from our Sense of Their Past?

John A. Vucetich, Rolf O. Peterson and M. P. Nelson

“It is the principle involved, and not its ultimate and very complex results, that we can alone attempt to grapple with.”
– Sir D’Arcy Thompson (1942:643)

INTRODUCTION

The wolves (*Canis lupus*) and moose (*Alces alces*) of Isle Royale have been studied continuously and intensively for nearly 50 years. In the context of informal settings (e.g., public talks and discussions with managers and colleagues), we have long characterized the most general conclusion of this long-term research in two ways. First, even after 50 years of observation, each five-year period of the wolf-moose chronology seems to be significantly different from every other five-year period. Second, the longer we study the more we seem to realize how poorly we understand the population dynamics of Isle Royale wolves and moose. In this paper, we pursue these ideas in a more rigorous fashion. The result may be insight, derived from long-term research, about how ecological explanations are developed and judged.

BACKGROUND

Natural history

Isle Royale emerged from Lake Superior (North America) over 8 K years ago. Isle Royale is a long (72 km) and narrow (~7.5 km) archipelago with one main island (544 km²) and approximately 150 smaller surrounding islands (most <0.1 km²). The island is located in Lake Superior, approximately 24 km from the Lake's north shore (Fig. 1.4.1). The island is almost completely forested. The topography is rough due to glacial scouring of ridges and valleys running the length of the island. Elevation ranges from 180 m to 238 m. The geologic history of Isle Royale is further described in Huber (1983).

The forest habitat is usefully characterized by three distinct regions. The northeast region is transitional boreal forest, dominated by spruce (*Picea glauca*), balsam fir (*Abies balsamea*), aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). The middle region was burned over in 1936 and is currently dominated by 80-year old stands of birch and spruce. The southwest region is covered with mixed stands of maple (*Acer saccharum*), yellow birch (*Betula allegheniensis*), cedar (*Thuja occidentalis*), and spruce. Swamps and other wetlands are common in the island's numerous valleys. The vegetation of Isle Royale, especially as it relates to moose herbivory, is further described in Pastor et al. (1998).

Moose arrived to Isle Royale in about the year 1900. Archaeological evidence from camps of Native Americans, who had used the island for at least the past 3K years, suggests that this was the first time moose had ever inhabited Isle Royale. Without reasonable evidence to the contrary, it is presumed that moose swam to Isle Royale. For 50 years moose interacted with the forest without predation or significant human harvest. By the late 1920s the impact of moose on the forest had become noticeable and the population probably comprised two or three thousand moose (Murie 1934). By the mid-1930s many moose had died of malnutrition and the population declined to probably a few hundred animals (Hickie 1936).

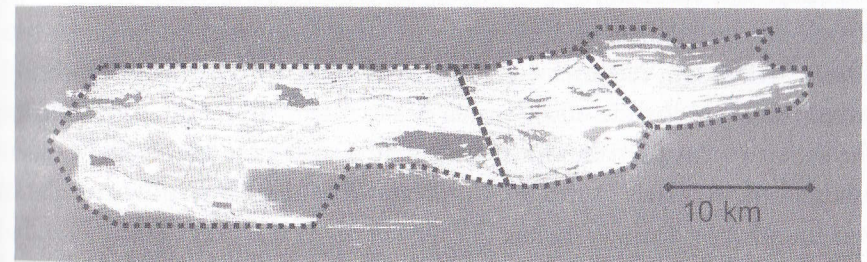
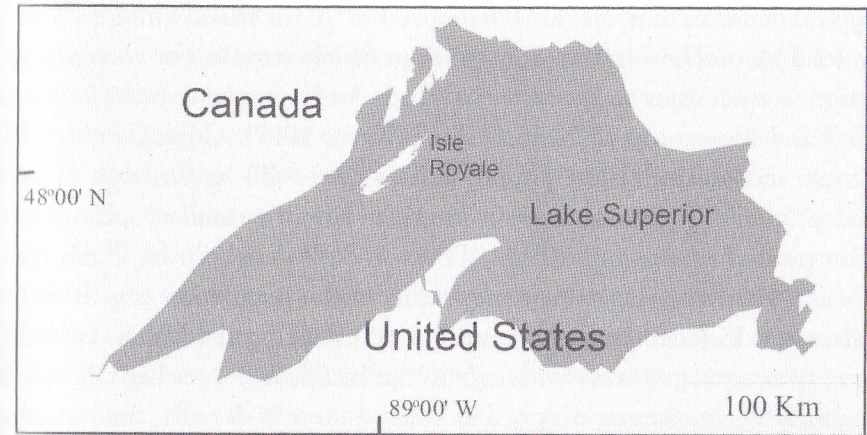


Figure 1.4.1. (a) The location of Isle Royale within Lake Superior, North America. (b) In this satellite image, Isle Royale is usefully divided into three regions. The middle region was largely burned in 1936, and is currently characterized by low moose density. The eastern third of Isle Royale and the western shoreline areas are transition boreal forest and characterized by higher moose density. The polygons denote the approximate boundaries of Isle Royale wolf packs in a typical year. Gray areas are inland lakes.

Murie (1934) suggested that the moose population be harvested or predators, such as wolves, be introduced as a means of controlling such boom and bust cycles. Murie (1935) was a strong advocate for wilderness preservation, and he believed neither of these interventions would be inconsistent with the notion of wilderness.

Isle Royale's moose density varies among the three basic habitat types. Typical densities in winter are 0.6 moose/km² in the island's middle region, and 2.5 moose/km² in the other portions of Isle Royale. For context, typical moose densities at other sites in North America tend to be <1.0 moose/km² and commonly <0.2 moose/km² (Karns 1997). Coincidentally, Isle Royale moose are relatively small-bodied (360–400 kg for adult females and 425–450 kg for adult males). They also have the smallest antler size of all measured moose populations (Peterson & Vucetich 2002). Each January and February, the average proportion of the population constituted of calves is 0.15 (coefficient of variation = 39). During the 1960s, twinning rates (proportion of cows with calves that had twins) were high (0.25). In the early 1970s, the rate dropped to ~0.10. In recent decades, the twinning rate has been less than ~0.05.

Although there were plans and one attempt to introduce wolves to Isle Royale in the 1940s and 1950s, the attempt failed and other plans were never carried out. Wolves arrived on Isle Royale by crossing an ice bridge connecting Isle Royale and Canada in the late 1940s. This is presumably the first time in the island's history that a wolf population had become established. Analysis of mtDNA indicates that the Isle Royale population was founded by a single female (Wayne et al. 1991). Since being founded, the Isle Royale population has remained genetically isolated. Empirical and analytical assessments suggest that the Isle Royale wolf population is extremely inbred, has lost ~80% of its neutral genetic diversity since being founded, and continues to lose ~13% of its neutral diversity each generation (i.e., the effective population size is ~3 and one wolf generation is ~4 years; Peterson et al. 1998).

The ultimate impact of inbreeding on Isle Royale wolves is unclear. Although Isle Royale wolves exhibit high rates of skeletal deformities (Räikkönen et al. 2006), whether fitness is affected by such deformities is unknown. Isle Royale wolves have vital rates (survival and recruitment) that are comparable with other healthy wolf populations (mean pack size = 4.9 [CV=47] for 1967–2006; mean number of pups in mid-winter = 3.0 [CV=90] for 1997–2006; mean annual mortality rate = 0.28 [CV=60] for 1975–2006). However, since 1980 the number of wolves for every

old (vulnerable) moose has been substantially less than before 1980 (Wilmers et al. 2006).

Humans do not harvest wolves, moose, or the forest. Although present on the nearby mainland, white-tailed deer (*Odocoileus virginianus*), coyotes (*C. latrans*), and black bear (*Ursus americanus*) are absent from Isle Royale. Winter wolf diet is ~95% moose, and summer wolf diet is >85% moose. Most of the remaining diet is beaver (*Castor canadensis*). The only significant causes of moose death are wolf predation and malnutrition, both of which are sometimes exacerbated by severe winters and winter ticks (*Dermacentor albipictus*). Between 40% and 60% of the moose winter diet is a single species (i.e., balsam fir). Compared with many large vertebrate communities, the Isle Royale wolf-moose system seems simple (Smith et al. 2003).

Moreover, the Isle Royale wolf-moose system is commonly characterized as a single-prey/single-predator system. However, the justification for this characterization is becoming increasingly difficult. The importance of other factors – such as canine parvo-virus (Wilmers et al. 2006), moose ticks (Peterson & Vucetich 2006), and winter severity (Vucetich et al. 2004) – have been made this clear.

Research history

Continuous research on Isle Royale wolves and moose began in the summer of 1958 (Fig. 1.4.2). At that time, the primary, long-term monitoring was an annual winter census of wolves and moose. Beginning in the early 1970s long-term monitoring expanded to include: 1) the key statistic that connects populations of predator and prey – the per capita kill rate, and 2) systematic and more concerted efforts to collect specific skeletal remains of dead moose (including skull, mandible, and metatarsus). Approximately one-third of all moose that have ever lived in the population are eventually collected, and currently we have skeletal remains of more than 4,000 different moose. By the mid-1990s, long-term monitoring had expanded again to include aspects of forest structure and demography (especially balsam fir tree-ring growth patterns, decline of canopy fir, and browse

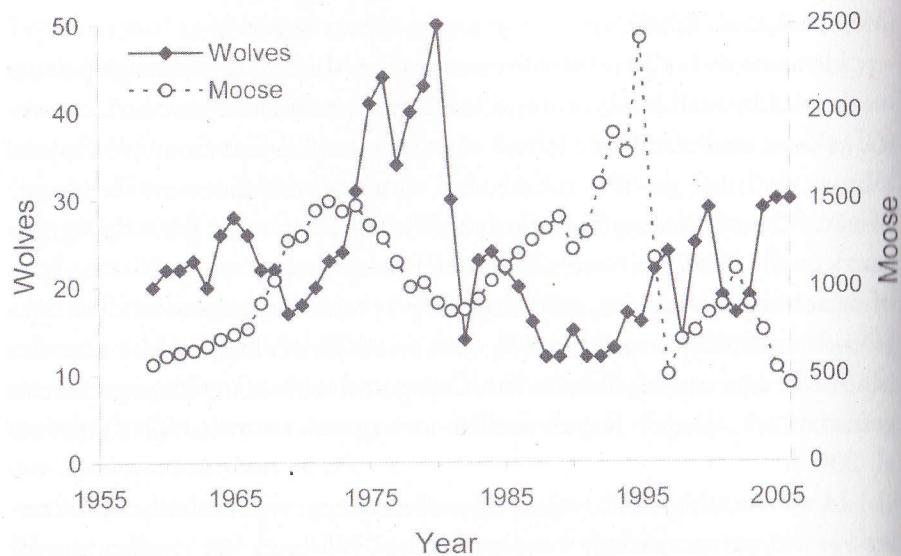


Figure 1.4.2. Population trajectories of wolves and moose on Isle Royale, 1959–2006. Each year the entire wolf population is counted from a small aircraft (details in Peterson & Page 1988). The number of moose is estimated from population reconstruction (before 1995, see Solberg et al. 1999) and aerial survey estimates (after 1995, details in Peterson & Page 1993).

rates). By 2005, long-term monitoring had expanded again to include annual monitoring of moose ticks, moose diet composition, and more intensive monitoring of wolf and moose genetics. Recently, we have also investigated the means by which moose forage quality and wolf intestinal parasites might be monitored annually. The greatest obstacle to continuing and expanding monitoring is limited funding, and the greatest resistance to improving the research is administrative.

NUMERICAL ANALYSIS

At the coarsest scale the interaction between wolf and moose populations can be characterized by the extent to which their abundances are correlated across years. Most generally, observational (i.e., non-experimental) ecological inquiry is fundamentally based on the observation and interpretation of covariation among temporally varying processes or entities. Undoubtedly, the interpretation can be complex and often entails autocorrelation and cross-correlation at various or multiple time lags (e.g., Pascual & Ellner 2000). Although we ignore such details in this analysis, we limit our inferences from this analysis (see below) to those we expect are robust to such simplification.

For no other purpose than as a heuristic, suppose that a simple explanation for a positive correlation is that prey largely determine predator abundance; a negative correlation may suggest that predators determine prey abundance, and weak correlation may indicate either a more complex interaction or weak interaction.

Between 1959 and 2006 the correlation between wolf and moose abundances was negative, but not strongly so ($r = -0.26$, $R^2 = 0.07$, $p = 0.08$). However, the estimated correlation has not always been such. Shorter-term correlations have fluctuated greatly throughout the first 50 years of the study.

To assess quantitatively how the estimated correlation has fluctuated over time, and how it has depended on the length of observation, we calculated a set of correlations, each depending on a different subset of the data. First, we estimated the correlation (and R^2) for each five-year, consecutive set of observations (e.g., 1959–1963, 1960–1964, ... 2002–2006). There are 44 such sets of data. Then we estimated the correlation (and R^2) for each 10-year, consecutive set of observations (e.g., 1959–1968, 1960–1969, ... 1997–2006). There are 39 such sets of data. We continued this procedure for sets of data that were 15, 20, 25, 30, 35, 40, 45, and 50 years in length. The result is depicted in Figure 1.4.3.

We appreciate that these data sets are not independent. We are careful to limit inferences drawn from this analysis (see below) to those that would

be insensitive to this lack of independence. Our inferences are motivated by appreciating that one could have observed the wolves and moose of Isle Royale beginning in any year and continuing for any period.

Estimated values of r range from nearly -1 to 1 , and instances of strong positive and strong negative correlation are common (Fig. 1.4.3a). The variation in r is substantially reduced for periods of observation that are 15 years and greater. The average R^2 declines with increasing periods of observation (Fig. 1.4.3b). Keep in mind, R^2 is sometimes taken as a measure of the explanatory power of a model.

Using the same subset of data described above, we also calculated estimates of the mean time to extinction (MTE) using a very simple model, requiring only knowledge about a population's past trajectory (Foley 1994). Our interest is not in MTE, *per se*. Rather, our interest in MTE is as a statistic that is sensitive to the estimated variance of a population's dynamics. Increased variance causes a decrease in MTE. The equation for MTE is (Foley 1994):

$$MTE = \frac{\exp(2ks)}{2sE[r]} (1 - \exp(-2sn_o)) - 2sn_o \quad (1)$$

where k is the natural logarithm of the carrying capacity (which we estimate as the maximum observed population to that point in the study), n_o is the natural logarithm of the most recent population size, s is the ratio $E[r]/\text{Var}[r]$ or the ratio of the expected annual population growth rate to the variance in the growth rate. The expectation and the variance were replaced with their maximum likelihood estimates based on the data observed for the particular subset of data being considered.

The relationship between duration of observation and MTE is complex, because with increasing period of observation there is a tendency for $\text{Var}[r]$ and k to increase (Arino & Pimm 1995). These factors have an opposing influence on MTE. Nevertheless, with increasing duration of observation the coefficient of variation in estimates of MTE decline

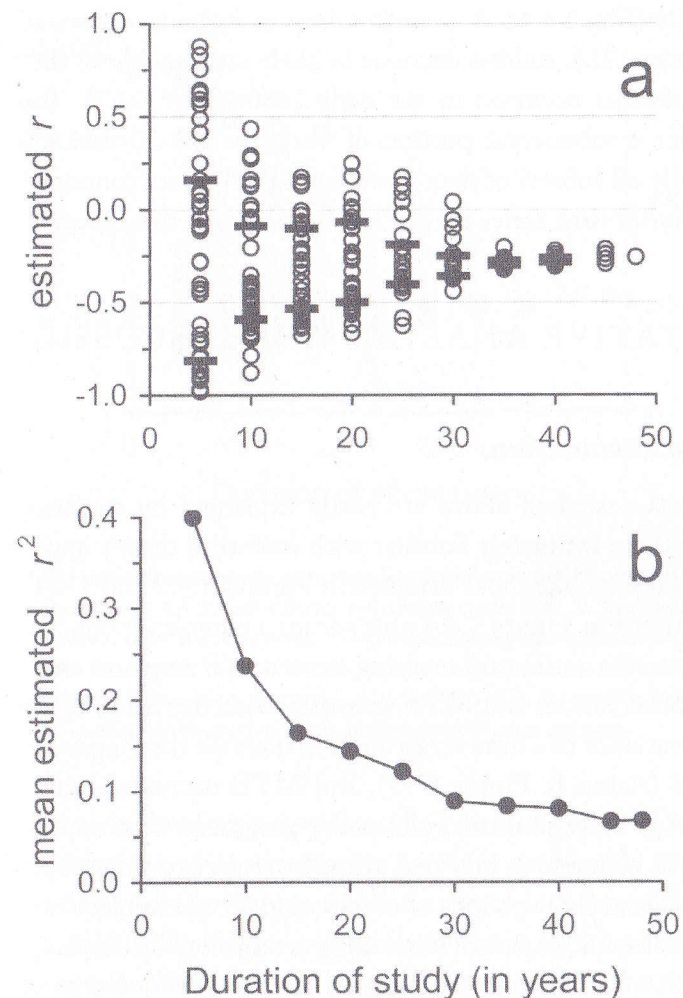


Figure 1.4.3. (a) Estimated correlation coefficient (r) between wolf and moose abundances across years (Fig. 1.4.2). Each estimate is based on a different subset from the time series of wolf and moose abundances. Each subset of data represents abundances from consequent years and is characterized by the number of years of observation (x -axis). Many of the data subsets are overlapping, and therefore not entirely independent. Heavy bars represent the interquartile range for each duration of observation. (b) Mean value of estimates for r^2 for the various subsets of data representing different durations of observation. Inasmuch as the r (panel a) represents a simple model of wolf-moose dynamics, r^2 represents the explanatory power of that simple model. Panel (b) suggests that with increased duration of observation, the explanatory power of this simple model tends to decline substantially over time.

dramatically (Fig. 1.4.4). A dramatic drop in variance occurs at 20 years of observation. This sudden decrease is likely attributable to the dramatic wolf decline that occurred in the early 1980s (Fig. 1.4.2). This decline accounts for a substantial portion of $\text{Var}[r]$ in the 50-year chronology, and virtually all subsets of data representing >20 years contain this event, whereas shorter time series may or may not contain this event.

QUALITATIVE ANALYSIS AND DISCUSSION

Statistical explanations

The patterns described above are easily explained by statistical theory. Moreover, those intimately familiar with statistical theory may even have anticipated results like those depicted in Figures 1.4.3 and 1.4.4.

The pattern in Figure 1.4.4 arises from a complex interaction of processes. First, the estimated carrying capacity (k) tends to increase with increased observation, and MTE increases with increased k . Second, the estimated variance of a time series tends to increase the longer a time series is observed (Arino & Pimm 1995), and MTE decreased with increased variance. Any ecological or evolutionary parameter that depends on the variance will be prone to bias that arises from underestimates of variance, which arise from short periods of observation. For example, demographic-based estimates for the rate of inbreeding are affected by the temporal variance in population abundance (Vucetich & Waite 1998). For processes that are highly autocorrelated (i.e., time series with reddened spectra), very long periods of time (perhaps more than one hundred years) may be required to accurately estimate the variance (Arino & Pimm 1995).

Figure 1.4.3 is vaguely explained by virtue of the wolf-moose system having been, apparently, a non-stationary process. Because stationarity is defined (informally, though adequately) as a process whose means, variances, and autocorrelation patterns are the same over whatever time interval they are observed; this account of Figure 1.4.3 may be more of a statistical description than an explanation.

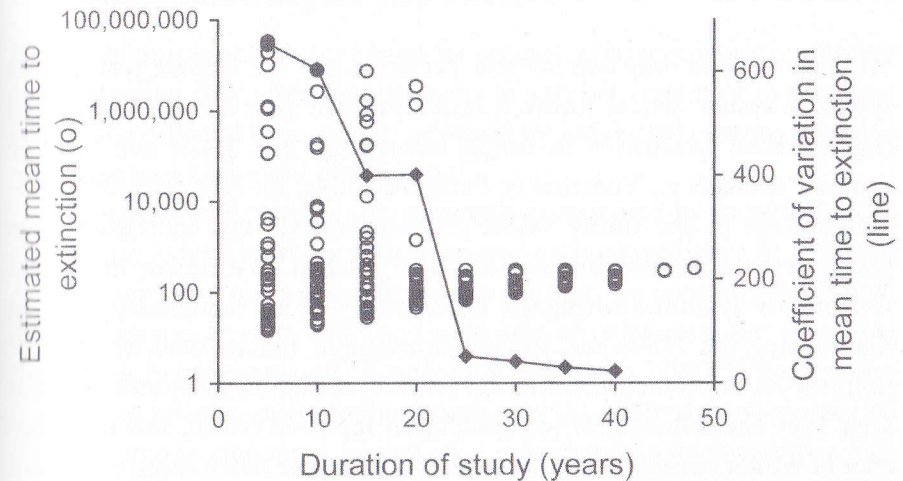


Figure 1.4.4. Estimated mean time to extinction based on population counts from the Isle Royale wolf population (Fig. 1.4.2) and a simple population model (Eq. 1). Each estimate is based on a different subset from the time series of wolf abundances. Each subset of data represents abundances from consequent years and is characterized by the number of years of observation (x -axis). Many of the data subsets are overlapping, and therefore not entirely independent. The solid line is the coefficient of variation for mean time to extinction estimates.

The low variance of responses (i.e., the y -axis of Figs. 1.4.3a and 1.4.4) for longer durations of observation is *partially* attributable to the longer time series being less numerous and more dependent on each other than the shorter time series (There are many five year segments with no data points in common). Variance for longer durations of observation could be higher than observed if more independent long time series were available. The explanation does not diminish the validity of the inferences we draw from Figs. 1.4.3 and 1.4.4 (see below).

Regardless of these statistical accounts, our observations are important for ecologists and managers whose sense of the world is more strongly influenced by empirical observation than by statistical theory. The critical question remains: how long does one have to observe an ecological system before it is stationary, before one can acquire a reliable sense of its functioning?

INDUCTION AND PREDICTIVE SCEPTICISM

We have studied only one 50-year period in the Isle Royale wolf-moose system, a system whose future is indefinite. The past 50 years have been characterized variously – in simple terms (e.g., Fig. 1.4.3) and in more complex terms (e.g., Vucetich & Peterson 2004a, b). Are there other 50-year periods in the future whose characterization will contradict these past characterizations? The idea is not far fetched. We already know that wolf-moose dynamics during the 1960s and 1970s are remarkably different than during the 1980s and 1990s. For example, before 1980 wolf predation was an important influence on moose population dynamics, whereas after 1980 the influence of wolf predation appeared trivial, and the influence of winter climate and food availability became much more important (Wilmers et al. 2006). Also, before 1980 there were about ~7 old moose per wolf (moose >9 years of age tend to be more vulnerable to predation), and since that time there have tended to be ~19 old moose per wolf (Fig. 5 of Peterson et al. 1998). If the first two decades of wolf-moose dynamics were quite unlike the two decades that followed, is it not plausible (perhaps even likely) that the next 50 years will be quite unlike the past 50 years?

Figure 1.4.3 and the previous discussion suggest a need for critically reconsidering the role of inductive reasoning in ecological science. Certainly, the role of inductive reasoning for extreme cases is reliably understood: It is reasonable to infer inductively that the next severe drought in a particular ecosystem will cause reduced primary productivity *because* severe drought usually causes reduced primary productivity in most studied ecosystems. At the other extreme, it is unreasonable to infer inductively that pine martens (*Martes americana*), for example, have a top-down effect on their prey because perch (*Perca fluviatilis*) have a top-down effect on their prey. Between these extremes there may be a significant set of ecological circumstances whereby inductive inference seems (even after careful consideration) to be reasonable, when in fact it is not.

Explaining past ecological phenomena

If the sole purpose of and criterion for ecological science is not to develop an explanation that *predicts* phenomena in another system or in the same system at a different time, then how would we judge explanations intended to explain past ecological phenomena?

Ecological explanations are commonly represented by statistical models that are judged by their parsimony *and* on how well they fit observed data. Importantly, measures of fit are *absolute* (e.g., for normally distributed data, R^2 ranges from 0 to 1), and measures of parsimony are *relative* to the models being compared (Burnham & Anderson 1998). When prediction is one's primary purpose then parsimony is a relatively well-developed concept: among compared models, the most parsimonious entails a balance between variance and bias that achieves confidence intervals with minimal width and coverage at the approximate nominal level. Hereafter, we refer to this as *narrow parsimony*. Examples of narrow parsimony include adjusted- R^2 and Akaike Information Criterion. Narrow parsimony can be expressed mathematically and typically includes a term to describe how well a model fits the observed data and a term to describe the model's complexity. Parsimony increases with increased fit and decreased model complexity.

Parsimony also has a more general sense, whose precise meaning is more difficult to isolate (e.g., Plutynski 2005). Explanations of past ecological phenomena ought to exhibit *general* parsimony, which may or may not correspond precisely with narrow parsimony. Below we discuss three Isle Royale examples that illustrate the issues that arise when explaining the past, rather than predicting the future, is the primary goal.

(1) Vucetich et al. (2002) compared several models aimed at explaining past patterns of the per capita rate at which wolves kill moose during winter. The most important comparisons were among these models:

$$\text{prey-dependent model: } \textit{kill rate} = \alpha N / (\beta + N) + \varepsilon, \quad (\text{Eq. 1a})$$

$$\text{ratio-dependent model: } \textit{kill rate} = \alpha(R) / (\beta + (R)) + \varepsilon, \quad (\text{Eq. 1b})$$

$$\text{predator-prey-dependent model: } \textit{kill rate} = \alpha N / (\beta N + P - \gamma) + \varepsilon, \quad (\text{Eq. 1c})$$

where N is moose abundance, P is wolf abundance, R is the ratio of moose to wolves, ε is an error term, and other Greek symbols are parameters estimated from data. Vucetich et al. (2002) concluded that the ratio-dependent model was the most parsimonious.

Conventionally, when narrow parsimony is quantified, model complexity is judged exclusively by the number of model parameters (i.e., dimensionality). However, a model's complexity also has a structural or conceptual component, which is not reflected by its dimensionality. Although the prey-dependent and ratio-dependent models are equally complex in terms of the numbers of parameters, the ratio-dependent model is conceptually more complex inasmuch as the predictor variable (i.e., the ratio of moose to wolves) is an interaction term. Because a bivariate predictor variable contains more information than a univariate predictor variable, the ratio-dependent model ought to (and does, in fact) outperform the prey-dependent model. The ratio-dependent model has a similar built-in advantage when compared to the model with both predator and prey abundance. Although both models account for the influence of wolves and moose, the ratio-dependent model does so with one fewer parameter. Does this set of candidate models represent a general strategy for developing better ecological explanations? That is, if two or more variables are expected to interact, should one combine them in some appropriate manner and omit the original univariate predictor variables? Such an approach would, if appropriate, be broadly applicable. Any related set of variables (e.g., climate variables) can be combined (using, e.g., principle components analysis) into some sort of interactive term. Is this a cheater's way of forcing more into a model without being penalized for the extra parameters, or is this a legitimate strategy for developing better explanations?

More generally, is it appropriate to compare the parsimony of a linear model (e.g., $y = a_0 + a_1 X$) with any of the various non-linear models that possess the same number of parameters as a linear expression (e.g., hyperbolic, inverse, exponential, or other such functions), or ought one to compare the linear model to a second order polynomial? The opportunity to express nonlinearity in X with one less parameter may allow one to justify an explanation with an additional predictor variable. For example, the expression, $y = (b_0 X_1 / (b_1 + X_1)) + b_2 X_2$, is nonlinear, has two predictor variables, and only three parameters (not including the variance of the error term), whereas a second order polynomial has the same number of parameters, but only one predictor variable. If one has good *a priori* reason to consider a simple linear model (with two parameters), then is special theoretical justification required to consider a nonlinear model (also with two parameters)? If such justification is available, would that not count as justification against considering the linear model? In this case the reason for tending so closely to the *a priori* considerations is that the non-linear model has a built-in advantage (i.e., it has increased complexity that is not accounted for by narrow parsimony).

An important sense of general parsimony is reflected by a corruption of an aphorism traditionally credited to Einstein: Scientific explanations ought to be as simple as possible, but no simpler. Under what conditions should a model (perhaps a model that exhibits narrow parsimony) be excluded from consideration as a useful explanation because it is too simple or ecologically inappropriate?¹ When should the seemingly objective, quantitative rational considerations associated with narrow parsimony be overridden by conflicting rational considerations?

Some think the prey-dependent model is a poor explanation, regardless of its empirical fit, because it implies certain properties that are undesirable (e.g., Akcakaya et al. 1995). Others think the same of the ratio-dependent model (e.g., Abrams 1994; see also Abrams & Ginzburg 2000). Perhaps the most critical shortcoming of the ratio-dependent model is that

¹ Burnham & Anderson (1998:140) discuss some negative consequences of even considering models that are inappropriate on a basis of *a priori* rational considerations.

it predicts that predators can persist in the presence of vanishingly small prey populations. In reality, there is some lower limit of prey below which a predator population cannot be supported. This pathology can be corrected by subtracting the lower limit (τ) from N (i.e., $kill\ rate = \alpha((N-\tau)/P)/(\beta+(N-\tau)/P) + \epsilon$). Although the data to which the model is being fit and the principles of narrow parsimony do not justify the inclusion of τ , it can be justified on the basis of observing, estimating, or guessing this lower limit from other knowledge. Is this a sensible means by which to develop an ecological explanation? Ecologists do not seem to agree on this matter (cf., Turchin 2003 and Boyce 2000 with Abrams 1994). The disagreement is fundamental and concerns understanding the proper balance between empirical observation and rational consideration in the development of explanations. Although rational considerations are a critical element of any explanation, the extent of their influence is not always easily identified, can be difficult to judge, and is prone to subjectivity.

(2) Vucetich and Peterson (2004a) examined two models that aimed to explain annual population growth rate in Isle Royale wolves. One model was more directly mechanistic (i.e., the predictor variable was per capita kill rate) and explained little observed variation (i.e., $R^2=0.22$). The other model was less directly mechanistic (i.e., the predictor variable was number of old, vulnerable moose) and explained more observed variation (i.e., $R^2=0.42$). If the purpose is to predict the future, clearly the second model seems more promising. However, if the purpose is to explain the past, how does one compare the explanatory value of a more mechanistic model that provides a poorer fit with a less directly mechanistic model, which happens to provide a better fit? Similarly, but more generally, consider a spectrum of modelling styles: from those relying more heavily on the inclusion of extra-empirical, though rationally justified, elements (e.g., Turchin 2003) to those focusing more on the development of inferences that can be supported primarily by the data upon which the model is primarily built, even if such data do not appear to exhibit aspects that may be rationally justified (e.g., Murdoch et al. 2003). Do they represent different kinds (of equally valid) ecological explanation, or does one style usually produce better or more useful ecological explanations?

If predicting the future is not a primary goal, then either/or approaches may not be the most appropriate means of developing ecological explanations (about past phenomena). If true, we may need a better understanding of how to develop unified explanations about ecological phenomena from various models and other bits of empirical information that seem incommensurable (Chapter 4 of Burnham & Anderson [1998] offer important advice about this issue, although it is limited to sets of models developed from exactly the same sets of data.)

(3) Vucetich and Peterson (2004b) attempted to explain how wolves, forage abundance, and climate affect the dynamics of moose. They used time series of moose abundance and other presumably related covariates (e.g., wolves, annual balsam fir growth, and climate). Given this context, compare:

$$moose_{t+1} = f(wolves_t, forage_t, climate_t) + \epsilon_t \quad (\text{eq. 2a})$$

with

$$moose_{t+1} = f(wolves_t, forage_t, climate_t, moose_t) + \epsilon_t \quad (\text{eq. 2b})$$

Suppose that inclusion of $moose_t$ (i.e., density dependence) affects the model in some important manner (e.g., increases the fit to the data and/or changes the parameter estimates associated with $wolves_t$, $forage_t$, and $climate_t$). If one's goal is to explain the past, rather than to predict the future, how, if at all, should the model with $moose_t$ even be considered? We do not dispute that understanding patterns of density dependence may be useful for certain purposes (e.g., predicting the future or comparing dynamics of different populations). However, if the goal is to understand how past patterns of moose abundance had been affected by predation or forage abundance, the inclusion of density dependent terms *could* result in a poor explanation for two reasons: (i) In advance we know that density-dependent dynamics are a necessary property of populations that persist and do not grow to infinity (Royama 1992). Consequently, in this context density dependence is a highly phenomenological process, without much potential to explain

anything beyond the population's persistence. (ii) Resource abundance and predation *may often* affect a population in an importantly density dependent manner. If so, density dependent terms will be confounded with resource and predation terms. Suppose one felt justified in giving primacy to the influence of *wolves_t*, *forage_t*, and *climate_t*, but still wished to judge whether previous moose abundance explained any additional variation in subsequent moose abundance. In this case, one might consider: *i*) fitting equation (2a) to the observed data, *ii*) fitting the time series of residuals from equation (2a) to the time series of previous year's moose density (i.e., fit this equation: $\varepsilon_t = g(\text{moose}_t) + \varepsilon'_t$), and *iii*) combining the two models: $\text{moose}_{t+1} = f(\text{wolves}_t, \text{forage}_t, \text{climate}_t) + g(\text{moose}_t) + \varepsilon'_t$. For emphasis, the parameters associated with *wolves_t*, *forage_t*, and *climate_t*, would be unaffected by $g(\text{moose}_t) + \varepsilon'_t$. This approach would assume that most density dependence in a population arises from interaction with predators and resources, rather than from territorial behaviour or interference intra-specific competition that is unrelated to food or predation.

This example reflects a very general issue concerning models that include sets of variables representing multiple levels of mechanism. To see the generality, suppose winter climate *per se* has little direct influence on moose population dynamics. Rather, suppose climate's effect is primarily indirect and affects moose through nutrition (food intake) and predation. In this case, one might construct a model that could be represented as: $\text{moose}_{t+1} = f(\text{wolves}_t, \text{forage}_t, \text{climate}_t) + h(\text{climate}_t) + g(\text{moose}_t) + \varepsilon''_t$. This approach is not obviously correct or incorrect, and not obviously better or worse than the kind of model represented by equation (2b).

When prediction is not the primary purpose of judging an explanation, then explanations may be primarily concerned with understanding causation. The notion of causation is surprisingly complicated (Skyrms 1980; Cartwright 1989; Pearl 2000). If severe winter climate causes moose to be more vulnerable to predation, and if predation causes moose abundance to decline, can we say that climate causes moose to decline? If one aims to develop ecological explanations in terms of cause and effect, then one must address how to combine the explanatory influence of variables that operate at different mechanistic levels.

Testing data or testing explanations?

Ecological data are difficult to collect. It is also often difficult to know when ecological data are collected with adequate precision or accuracy. Consequently, ecologists may often not know whether we are testing the adequacy of an ecological explanation, or testing the adequacy of data.

For example, how adequate is our perceived influence of balsam fir on moose population dynamics (i.e., Vucetich and Peterson 2004b; Wilmers et al. 2006)? We represent balsam fir by an annual index of tree-ring growth, which is thought to reflect annual primary productivity. Do we underestimate the influence of balsam fir because tree-ring growth is a poor indicator of balsam fir availability? Do we overestimate the influence of balsam fir because fir growth is highly correlated with the availability of other unmeasured forage?

Similarly, if adequate ecological explanations are relatively complex (recall Einstein's aphorism), then the development of adequate explanations requires data from numerous potentially related processes collected over long periods. This is an important issue, because we do not know if adequate ecological explanations are relatively complex (cf., Burnham & Anderson 1998:12 and Kareiva 1994), and the data necessary to test relatively complex explanations is remarkably sparse.

There is a huge difference between testing data and testing explanations. In many cases, one gets the sense that ecologists believe we are testing explanations, when in fact we are confirming the inadequacy of our data to test potentially adequate explanations.

Ecological explanations and historical explanations

The timing and circumstances of the collapse of the Soviet Union were unpredicted. Nevertheless, there are reasonable explanations for the cause of the collapse. Human history is importantly represented by events that were unpredicted but were subsequently provided with reasonable explanations. The history of the Isle Royale wolf-moose chronology is comparable. The severity of the wolf collapse of the early 1980s was not predicted (Fig. 1.4.2). Nevertheless, introduction of canine parvovirus is a reasonable explanation

for the decline (Peterson et al. 1998). The severity of the moose collapse in the mid-1990s was not predicted. Nevertheless, there is a reasonable explanation (i.e., convergence of severe winter, moose tick outbreak, lack of forage, exceptionally high moose density).

If pure predictive ability is not the sole (or primary) determinant of what counts as a good ecological explanation about past ecological phenomena, then this may be one way in which ecology differs fundamentally from a science like physics, where prediction is generally treated as necessary and paramount. Good explanations of past ecological events may be like good explanations of past events in human history. Epistemologically, ecology may be like a hybrid of physics and systematic investigations of human history.

Importantly, the criteria for good explanations in history may be quite different than is the case for physics. An important, caution-raising implication of relating ecology to history is that the primary purpose of explaining human history may be fundamentally political and ethical – that is, for the purpose of prescribing how we ought to behave and relate to other humans (Staloff 1998; Lemon 2003). Is the general and fundamental purpose of explaining ecological phenomena to prescribe how we ought to interact with nature? If it is, should it be? Can it be otherwise? Is the prescriptive dimension of ecological explanations substantial and inescapable – as is often the case for historical explanations?

Certainly, consulting an ecologist about how to manage natural resources (i.e., science-based management) is analogous to consulting a physicist about how to build a spacecraft. However, to what extent is such ecological consultation analogous to consulting a historian about how to run a government? The nature of the physicist's advice depends only on her knowledge. The nature of the historian's advice depends on the historian's knowledge, political tendencies, and ethical attitudes. Arthur Schlesinger, Jr., William F. Buckley, and Arthur Herman are all highly qualified historians/political scientists, but each would have critically different views on how to run a government. No respectable politician should defend his or her use of a historian's advice on the sole basis that the historian is

knowledgeable about history. How exactly ought natural resource managers relate to ecologists?

Predicting future ecological phenomena

If inductive reasoning about future ecological phenomena is *sometimes* unreliable, and if we have a poor *a priori* sense for knowing when induction is and is not unreliable, then how ought natural resource managers interact with ecological systems? We are not championing an extreme notion of scepticism, whereby inductive reasoning about future ecological phenomena is always unreliable. Our claim is that for a significant set of cases, inductive reasoning will not be reasonable, though it may seem so. The Isle Royale chronology illustrates this possibility inasmuch as there are numerous five- and ten-year periods whereby one would have gotten the false sense that wolf and moose abundance is strongly correlated (Fig. 1.4.3).

In principle, natural resource managers conventionally rely on two tools for decision making in the face of uncertainty, adaptive management (AM; Walters & Hilborn 1978), and risk analysis (RA; Varis & Kuikka 1999; Byrd & Cothorn 2000). What kind of tool is AM, if the future is often unlike one's empirical sense of the past? If one's sense of the past is based on short periods of observation,² then AM may not be particularly useful. Conversely, AM would not seem all that effective a tool if reconsideration of a management action were held off until a reliable sense of its effect is available, which may take 30, 50, or more years of observation. If one has good reason to think that the future is often unlike one's empirical sense of the past, then RA is difficult to employ because there is little empirical basis for judging the probabilities of various outcomes, given various actions.

Although AM and RA may be necessary components of reliable management, they may not be sufficient. The Isle Royale experience, like many other experiences, suggests that the Precautionary Principle (deFur & Kaszuba 2002) is also necessary. Because we often have a poor sense of

² Imagine an adaptive management program where the evaluation of management required 50 years of observation.

the magnitude of our ignorance, the Precautionary Principle may be necessary when uncertainty and ignorance are thought to be great *and* when they are thought to be unimportant. To quote Oliver Wendell Holmes (Simmons 1992): "*Certitude is not the test of certainty. We have been cocksure of many things that are not so.*" Consequently, the challenge presented by the Precautionary Principle is not understanding when it should be applied – it should always be applied. Rather, the underappreciated challenge of the Precautionary Principle is to understand what it suggests that we actually do (see Majone 2002; Conko 2003; Goldstein & Carruth 2005). Better understanding of the Precautionary Principle will require committed collaboration amongst sociologists, environmental philosophers, political scientists, and ecologists.

Finally, the Precautionary Principle may often be motivated by fear that mismanagement of natural resources will be detrimental to human "welfare" and enterprises. Ethical considerations (e.g., Taylor 1986; Naess 1989; Callicott 1999) and the influence on the emotional intellect (Goleman 2005) of many people who reflect on the Isle Royale ecosystem (personal observation) suggest that even the Precautionary Principle, because of its relation to fear and focus on human welfare, could be inadequate for developing a right relationship with nature. A reasonable case can be made that a right relationship with nature requires "natural resource management" that arises from respect for and wonderment at nature's intrinsic value (Moore 2005), rather than fear of nature's revolt against humanity. Differences between a management based on fear and one based on wonder and respect are liable to be substantial.

Extreme events and causal explanations

Extreme events (e.g., so-called "100-year droughts") may have substantial impacts on a population, especially if relationships are highly nonlinear at extreme ends of a predictor variable's range. Understanding the impact of extreme events may be difficult, because extreme events are thought to occur only rarely.

However, the frequency of extreme events depends on one's perspective. One could recognize numerous types of independently occurring extreme events, each of which are able to influence a moose or wolf population's dynamics (e.g., summer temperature, timing of green-up, annual snow fall, a few types of disease, etc.). If there are 10 independent variables and the probability of a single extreme event is 2% (e.g., extremely severe *or* extremely mild winter), then some kind of extreme event (i.e., something comparable to, say, a "100-year drought") occurs, on average, about once every 6 years. Moreover, two extreme events could co-occur in the same year. Co-occurring extreme events could have similar or opposing influences on the population, and may or may not interact (in the statistical sense of the word). If there are 10 independent variables and the probability of any single extreme event is 4% (e.g., extremely severe *or* extremely mild winter), then two extreme events (i.e., each comparable to, say, a "50-year drought") co-occur, on average, about once every 20 years.

In nearly five decades of observing the wolves and moose of Isle Royale, we are aware of several extreme events. In the early 1980s, the wolf population crashed in response to canine parvovirus. In the mid-1990s, the moose population crashed during the coincidence of an extremely severe winter, extremely low forage abundance, and a moderate outbreak of ticks. In the early 2000s, moose were negatively affected (and wolves were positively affected) by what may turn out to be a severe multi-year outbreak of ticks. In 2005, moose may have been adversely affected by an extremely hot summer.

The challenge presented by extreme events is: Because a particular type of extreme event occurs rarely, its impact is difficult to understand. This creates substantial difficulty in knowing whether a population is primarily affected by many different types of extreme effects or by moderate variation in a few key effects. This alternative represents a very basic feature of a population's dynamics, about which ecologists seem to have divergent opinions (cf., Burnham & Anderson 1998:12 and Kareiva 1994). Using conventional principles of model selection, a fair empirical comparison of this alternative is not possible unless a system has been observed for a very long time. For organisms in seasonal environments, a long time (measured

in years) is about ten times the number of possible effects. The inability to assess this alternative empirically heightens any insight that might arise from a conceptual assessment.

The *number of effects* required to adequately describe a population depends not only on the contingent, empirical nature of the population, but also on the purpose of the model (i.e., predicting future or explaining past) and the logical constraints implied by the *kind of effects* that one considers. When one's purpose is prediction of unobserved (future) events, then conventional model selection strategies based on narrow parsimony are appropriate. In this case, models with fewer parameters will usually be selected in favour of modes with more parameters, not because the simpler models are adequate, but because the sample size is small (duration of observation is short).³

When one's purpose is to explain the past, model development is more complex. As an illustration, compare this set of models:

$$r_t = \alpha_0 + \alpha_1 m_t + \varepsilon_t \quad (3a)$$

$$r_t = \alpha_0 + \alpha_1 w_t + \varepsilon_t \quad (3b)$$

where r_t is moose population growth rate in year t , m_t is moose density, w_t is wolf density, ε_t is usually referred to as the error term, and the alphas are coefficients estimated from the data.

Equation 3a is the simplest, least mechanistic, and most general model in population biology. The first two terms of equation 3a describe how the population is *affected* by numerous density-dependent *effects*, and the third term describes the affect of numerous density-independent effects. Logically, all possible effects are accounted for (albeit phenomenologically) by the two mutually exclusive sets of terms. Even if the so-called model fit is low (i.e., low R^2), the model is perfectly adequate for explaining how

past dynamics have been influenced by density-dependent and density-independent effects.

Although equation 3b entails more mechanism than equation 3a, it is odd in a certain way. The first two terms of equation 3b describe the effect of predation, and the third term accounts for effects that are not predation. Although this set (predation and not predation) is mutually exclusive and covers all possible effects, it is an odd way to sort the universe of possible effects. Conceptually, it may be necessary (and possibly sufficient) to account for moose forage if one accounts for predation. If so, the universe of possible effects is divided and completely covered by three categories: predation, forage, and other effects. If accounting for predation requires accounting for other effects representing a similar level of mechanistic detail, then failure to do so may result in a misspecified model (i.e., a model that omits an important variable). Misspecified models have biased parameter estimates, unless the omitted variable(s) is completely orthogonal (uncorrelated) to the observed variable(s) (Phillipi 1993).

The comparison of equations 3a and 3b suggests that the number of variables needed to describe adequately a population depends importantly on how one divides the universe of possible effects, as opposed to depending exclusively on empirical, contingent aspects of the population being analyzed. Inclusion of a mechanistic term may imply the need to include all mechanisms occurring at that level of detail, if biased estimates of model coefficients are to be avoided. It also seems likely that mechanisms that are more detailed will be associated with a larger set of other mechanisms that operate at the same level of detail.

This comparison of equations 3a and 3b also implies a conceptual deficiency with an equation like $r_t = \alpha_0 + \alpha_1 m_t + \alpha_2 w_t + \varepsilon_t$. Consider this equation to be an elaboration of equation 3a. If predation has elements that are density-dependent and (or) density-independent, then the terms of this equation do not represent a set of mutually exclusive categories. The result is a confounded set of parameters.

Our assessment of equation 3b showed that mechanistic models might be vulnerable to biased parameter estimates. Although a model with biased parameter estimates may fit observed data well, such a model would, by

3 Sample size limits the number of parameters that can be estimated with reasonable precision (i.e., reasonably small standard error). When a parameter estimate is associated with a large standard error, the estimate may be a poor reflection of the truth.

definition, provide a distorted sense of causal influence. Moreover, an accurate sense of causal influence would seem an essential component of a good explanation, especially if prediction is not paramount. However, the conceptual nature of causation is sufficiently elusive, especially for observational data gathered in an ecological context, that a more sophisticated appreciation is needed. There are good reasons for thinking that formal experimentation is the only practical means by which causation may be determined (e.g., Havens & Aumen 2000; Fowler et al. 2006; cf. Pearl 2000), and for thinking that causation does not even exist unless there is an external manipulator (e.g., Russell 1913; Holland 1986). The best explanations of the Isle Royale wolf-moose system may not be primarily concerned with an external manipulator. Because causality is a sufficiently vexing concept, it seems reasonable to admit explanations of past ecological phenomena that do not depend importantly on any notion of causation. Good explanations of past ecological phenomena may entail no more than a model that is rationally reasonable and provides a good empirical fit – regardless of its causal accuracy (or narrow parsimony) (Thompson 1942; Keller 2002).

The development of ecological explanations

Scientific explanations may be usefully characterized by their degree of simplicity or complexity. The virtue of complex explanations is our belief that nature is complex. The virtue of simple explanations is their comprehensibility, testability, and applicability. Scientific explanations also arise from a dialectic between *a priori* rational considerations (i.e., theories) and empirical observation.⁴ The duration of empirical observation may generally limit the complexity (or simplicity) of many ecological explanations. The Isle Royale study may illustrate something general about how ecological ideas develop.

4 This view is consistent with most modern philosophers of science (e.g., Kuhn 1962; Laudan 1990; Brown 2001; Rosenberg 2005). This view contrasts with K. Popper's (1959) view, that science entails two highly distinct stages: hypothesis generation and hypothesis testing. Hypothesis testing is a purely empirical affair, and hypothesis generation could arise from any rational (or irrational) process.

The relationships illustrated in Figure 1.4.3 suggest that short-term research (e.g., studies <10 years) would often promote belief in simple ideas (e.g., a strong bivariate correlation and high R^2). Moreover, short-term research would tend to preclude the development of complex ideas; because, in the context of multiple regressions, detecting the influence of even moderately important predictor variables requires about ten observations per predictor variable (i.e., a model with five predictor variables may require upwards of 50 observations).

In the parlance of Frequentist statistical theory, precluding the development of a complex idea is analogous to a Type II error, and belief in simple ideas is analogous to a Type I error. Unfortunately, short-term research can foster errors of both types simultaneously. By contrast, long-term research may allow for the development of more complex ideas, and usually discredits belief in simple ideas. One guard against becoming overly convinced about the appropriateness of a simple idea is to calculate and report confidence intervals for R^2 (Neter et al. 1989). Although this is rarely done, it can be illustrative. For $n=50$, the 90% CI for $R^2=0.5$ is approximately [0.32, 0.65]. For $n=25$, the 90% CI for $R^2=0.5$ is [0.24, 0.71]. This method of calculating CI's is not advisable for $n<25$.

A similar sense about the influence of duration of observation is implied by comparing ideas that have arisen at various points in the history of the Isle Royale study. After observing Isle Royale wolves and moose for less than five years, Allen and Mech (1963) concluded: "*Our studies thus far indicate that the moose and wolf populations on Isle Royale have struck a reasonably good balance.*" Today, "reasonably good balance" seems like an inadequate description of the Isle Royale system. More recently, the Isle Royale dynamics have been characterized by comparison to "discordant harmonies" (Botkin 1992).

After a few years of observation, Mech (1966) concluded that wolf predation reduced moose abundance to levels below which resources limited moose populations. After about 15 years of observation, Peterson (1977) concluded that food limitation did affect moose population dynamics, as did annual fluctuations in winter severity. Only after nearly 50 years of observation has disease been implicated in affecting long-term dynamics

of Isle Royale wolves and moose (Wilmers et al. 2006). Most recently, we are beginning to suspect that moose ticks also play an important role in long-term wolf moose dynamics (Peterson & Vucetich 2006). We are just now attempting to develop means for long-term monitoring of forage quality and summer forage for moose.

Beginning about 70 years ago, a central tenet of predation ecology has been that the kill rate is largely determined by biological processes (i.e., prey abundance or the ratio of prey to predator), and is the primary predictor of predator growth rate. Based on approximately 30 years of observation, Vucetich et al. (2002) and Vucetich and Peterson (2004a) concluded that Isle Royale wolf kill rate was: (i) poorly predicted by moose abundance or the number of moose per wolf and (ii) did not provide a good basis for predicting population growth rate of Isle Royale wolves.

D'Arcy Thompson and the nature of explanation

The distinction we make between predicting the future and explaining the past for population ecology is, at the very least, congruent with D'Arcy Thompson's view on the nature of biological explanations. Thompson is known as the father of mathematical biology and for his magnum opus, *On Growth and Form* (1942). *On Growth and Form* is a classic because its depiction of what counts as a biological explanation is attractive to some and bewitching to, but not easily dismissed by, others (Keller 2002). The most succinct expressions of Thompson's (1942) view on the nature of biological explanations seem to be: "*It is the principle involved, and not its ultimate and very complex results, that we can alone attempt to grapple with.*" Thompson (1942) also writes (p. 75):

"We must learn from the mathematician to eliminate and to discard; to keep the type in mind and leave the single case, with all its accidents, alone; and to find in this sacrifice of what matters little and conservation of what matters much one of the peculiar excellences of the method of mathematics."

Thompson (1942) seems to have thought that (Keller 2002): "The representation of living processes in mathematical form might have utilitarian value, but it could also be viewed as an end in itself." Keller (2002) explains Thompson's mathematical end-in-itself this way:

"[Thompson] may have faulted the founding father of morphology [Goethe] for ruling "mathematics out of place in natural history," but he was more than sympathetic to Goethe's criticism of the constraint exerted on man's ability to understand the world of nature by the "compulsion to bring what he finds there under his control." In [Thompson's] view, the best and highest uses of mathematics lay well beyond the range of that compulsion; indeed it was mathematics that would lead us along the path that Goethe himself had advocated – to a proper appreciation of the "variety of relationships livingly interwoven" [Thompson quoting Goethe].

Keller (2002) also describes Thompson's view on explanations in terms that imply the reality of particulars (whose complex results cannot be grappled with) and the less certain nature of principles that can be grappled with:

"For Thompson, the goal of explanation appears to have been primarily one of sufficiency – in only a few instances did he argue for logical necessity, and virtually never for empirical necessity. He said in effect, this is how it could happen, not how it need happen, and certainly not how it does happen in any particular instance. One might say that what he found most compelling about mathematics was not so much its deductive power as its power to lead our imagination away from the particular instances found in the real world and toward that which the particular is a mere instance."

Keller (2002) concludes:

“In comparing Thompson’s explanatory goals with those of classical geneticists, I remarked on the different values placed on necessity and sufficiency... Such differences, I claim, demarcate distinctive epistemological cultures in the practice of science.”

Keller’s evidence suggests that recent and contemporary science is comprised of various epistemological cultures. More specifically, the value of various kinds of explanation varies among scientific cultures. Despite the divergence, each view is a scientific view, by virtue of being held by a scientific community. In this sense it may not be all that valuable to consider whether the epistemological culture of applied ecology is scientific. However, it is critical to ask whether the epistemological culture of applied ecology – a culture confident in its aim to predict future ecological phenomena – is one that promotes a flourishing relationship between humans and nature.

CONCLUSION

Hypotheses about the wolves and moose of Isle Royale have been generated by observing that system (e.g., Mech 1966). These hypotheses have been rejected by continuing to observe the wolves and moose of Isle Royale (e.g., Peterson 1977). This process of observation and rejection causes us to wonder about the limits of inductive reasoning in population ecology and whether the future of Isle Royale wolves and moose will always differ from our sense of their past. In plainer language, albeit with the loss of some important detail: even after 50 years of observation, each five-year period of the Isle Royale wolf-moose chronology seems importantly different from every other five-year period (Fig. 1.4.1). More strikingly, the first two decades of observation (1959–1980) are characterized by markedly different dynamics than those of the following two decades (Fig. 5 of Peterson et al. 1998; Wilmers et al. 2006).

Nearly 50 years of observation were required to conclude that long-held cornerstones of quantitative predator-prey theory are inadequate for predicting future Isle Royale wolf-moose dynamics. Specifically, per capita kill rate is not well predicted by prey density (Vucetich et al. 2002), and wolf growth rate is not well predicted by kill rate (Vucetich and Peterson 2004a).

Our characterization – that the longer we study the wolves and moose of Isle Royale the more we learn how little we understand – seems reasonable if understanding is judged primarily on the ability to make reliable, nontrivial predictions about the future dynamics of populations. When predictive ability is the judge of knowledge, the growth of ecological knowledge may be a process of discovering ignorance.

Because, as the Isle Royale system suggests, inductive reasoning about ecological systems may frequently be unreliable, it may be necessary to distinguish two types of ecological explanation: those entailing predictive ability and those entailing non-predictive explanations of the past.

When the value of an explanation is not based solely on predictive ability, its value is judged on a delicate mixture of empirical observation and rational consideration. The rational considerations will, at times, seem (at least, to outside observers) to be subjective conclusions of researchers and (or) peer-reviewers. The meaning of empirical observations is deeply dependent upon rational and theoretical presuppositions that are not always easily identified or justified to the point of excluding conflicting presuppositions.

With respect to explaining the past, much understanding has been gained. We have learned that wolves are selective predators (Peterson 1977), social structure is an important determinant of predation rate (Thurber & Peterson 1993), a disease-induced reduction in wolf abundance was followed by increased moose abundance and reduced growth of balsam fir (McLaren & Peterson 1994), and raven scavenging may favour sociality in wolves (Vucetich et al. 2004). Although this knowledge may have limited value for predicting the future, it seems necessary and sufficient for providing a reasonable (albeit, incomplete) explanation of the past. They lead us,

in the words of D'Arcy Thompson and Goethe, to "*a proper appreciation of the variety of relationships livingly interwoven.*"

ACKNOWLEDGMENTS

We thank L. Vucetich for comments on previous draft of this manuscript. This work was supported in part by the U. S. National Science Foundation (DEB-9903671 and DEB-0424562) and Isle Royale National Park. This chapter does not necessarily reflect the views of the NSF or Isle Royale National Park.