

Chapter 3

Wolf and Moose Dynamics on Isle Royale

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3.1 Background

Moose (*Alces alces*) arrived on Isle Royale in the early 1900s (Mech 1966). For 50 years moose interacted with the forest without being exposed to predation or significant human harvest. By the late-1920s the impact of moose on the forest had become noticeable and the population probably comprised between 2,000 and 3,000 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).

Although there were suggestions and one attempt to introduce gray wolves (*Canis lupus*) to Isle Royale in the 1940s and 1950s, the attempt failed in 1952 (Mech 1966). While humans were trying to reintroduce wolves, they arrived on their own in the late 1940s by crossing an ice bridge connecting Isle Royale and Canada. Analysis of mitochondrial deoxyribonucleic acid (mtDNA) indicated that the population of wolves on Isle Royale was founded by a single female (Wayne et al. 1991). Since the founding event, the wolf population on Isle Royale has, to our knowledge, remained genetically isolated.

Humans do not harvest the wolves, moose, or forest on Isle Royale. Although present on the nearby mainland, white-tailed deer (*Odocoileus virginianus*), coyotes (*Canis latrans*), and black bears (*Ursus americanus*) are absent from Isle Royale. The diet of Isle Royale wolves is ~95% moose during winter, and the diet in summer is >85% moose. Most of the remaining diet consists of beavers (*Castor canadensis*). The only significant causes of death for moose on Isle Royale 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 diet of moose in winter is a single species, balsam fir (*Abies balsamea*).

Although the wolf–moose system on Isle Royale is commonly characterized as a single-prey/single-predator system, this characterization may not be entirely justified. The importance of other factors such as canine parvovirus (Wilmers et al. 2006), moose ticks (Peterson and Vucetich 2006), and winter severity (Vucetich and Peterson 2004a) have been clearly documented. Nevertheless, compared with many communities of large vertebrates, the wolf–moose system on Isle Royale seems simple (Smith et al. 2003).

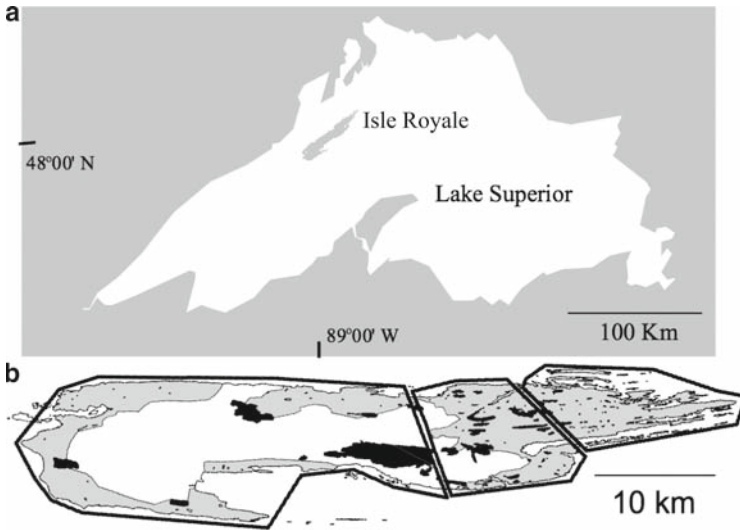


Fig. 3.1 **a** The location of Isle Royale within Lake Superior, North America. **b** Isle Royale is in most years inhabited by three wolf packs, whose typical territorial boundaries are indicated by the *thick-lined polygons*. The *gray regions* of the island represent area with higher moose density. The *white region* is roughly associated with a forest fire that burned in 1936. *Black areas* are inland lakes

Isle Royale is a long (72 km) and narrow (~7.5 km) archipelago with one main island (544 km²) and ~150 smaller surrounding islands (most <0.1 km²). The island is located in Lake Superior, ~24 km from the Lake's north shore (Fig. 3.1). 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 above sea level.

The island is almost completely forested. The island's forests are usefully characterized by three distinct regions. The northeast region is transitional boreal forest, dominated by spruce (*Picea glauca*), balsam fir, aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). The middle region was burned 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 numerous valleys on the island, but are more numerous in the eastern two-thirds of Isle Royale. The vegetation of Isle Royale, especially as it relates to moose herbivory, is further described in Pastor et al. (1998).

3.1.1 History of Research on Isle Royale

Continuous research on the wolves and moose of Isle Royale began in the summer of 1958 (Fig. 3.2). At that time, the research was primarily based on an annual winter census of wolves and moose. Beginning in the early 1970s, long-term

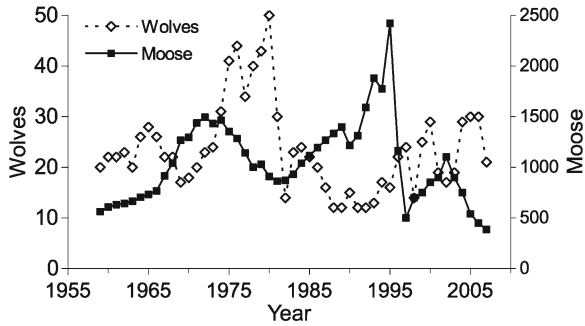


Fig. 3.2 Population trajectories of wolves and moose on Isle Royale, 1959–2007. Each year the entire wolf population is counted from a small aircraft (details in Peterson and Page 1988). The number of moose is estimated from population reconstruction (prior to 1995, see Solberg et al. 1999) and aerial surveys (after 1995, details in Peterson and Page 1993)

monitoring expanded to include per capita kill rate – a key statistic connecting populations of predator and prey – and systematic and more concerted effort to collect specific skeletal remains of dead moose (including skull, mandible, and metatarsus). The skeletal remains of approximately one-third of all moose that have ever lived in the population are eventually sampled; 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 tree-ring growth patterns of balsam fir).

3.1.2 Some Basic Demography

The density of moose on Isle Royale 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 habitat types at the east and west ends 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). Each January and February, calves represent 15% of the population, on average (coefficient of variation = 0.39). 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.

Empirical and analytical assessments suggest that the wolf population on Isle Royale 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 approximately three, and one wolf generation is ~4 years; Peterson et al. 1998). The ultimate impact of inbreeding on the wolves of Isle Royale is unclear. Although wolves on Isle Royale exhibit high rates of skeletal

deformities (J. Rääkkönen et al., unpublished data), whether fitness is affected by such deformities is unknown. Wolves on Isle Royale have vital rates (survival and recruitment) that are comparable with other healthy wolf populations (mean pack size = 4.9 [Coefficient of variation {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 (Vucetich and Peterson 2004b).

3.2 Some Perspectives from Isle Royale

Here we present an annotated list of observations and inferences derived from studies of the wolves and moose of Isle Royale.

1. *The functional response and numerical response, fundamental elements of conventional predator–prey theory, represent inadequate bases for understanding kill rates and wolf–moose dynamics.*

The density of prey populations and the prey:predator ratio each have an important influence on per capita kill rate (Fig. 3.3a, b). This empirical finding conflicts with several models for Isle Royale wolves and moose that have assumed otherwise (e.g., Eberhardt 1997). However, “having an important influence” is critically different than claiming kill rate is adequately understood or predictable (contra Messier 1994). Because neither prey density nor prey:predator ratio predict more than about one-third of the variation in kill rate, neither seems adequate for understanding annual fluctuations in kill rate. Similarly, with respect to the numerical response, the kill rate explains about 22% of the variation in wolf population growth rate (Fig. 3.3c; Vucetich and Peterson 2004c). Clearly, kill rate has an important influence on growth rate of the wolf population. However, to merely identify kill rate as an important influence is far from concluding that one can reliably predict growth rate of the wolf population from kill rate. This ability is still beyond our reach, at least for Isle Royale wolves.

Much of the unexplained variation in kill rate and growth rate of the wolf population is likely attributable to factors such as climatic variation, age structure of the moose population, sampling error (in the measurement of kill rates), demographic stochasticity (Vucetich and Peterson 2004b), and behavioral factors such as pack size, experience, and leadership. The prospects for predicting some of these factors (e.g., annual climate) are severely limited.

The poverty of these relationships is meaningful because the functional response (Fig. 3.3a, b) and the numerical response (Fig. 3.3c) are the fundamental elements of conventional predator–prey theory. An important approach to predicting population dynamics is to assemble mechanisms such as the functional response and numerical response into a population model for the purpose of better understanding or predicting predator–prey dynamics (Messier 1994; Turchin 2003; Varley and Boyce 2006).

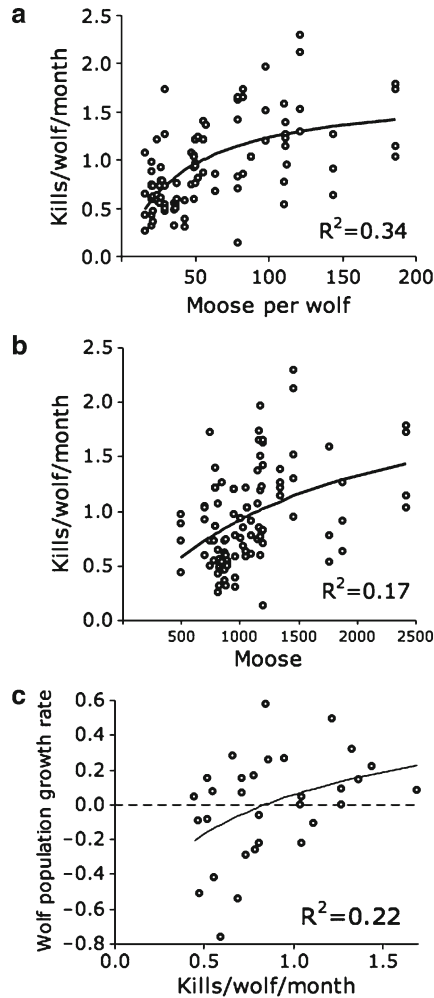


Fig. 3.3 The relationship between moose per wolf and per capita kill rate (a), the functional response (b), and numerical response (c) for wolves and moose on Isle Royale. Panels (a) and (b) are adapted from Vucetich et al. 2002, depict pack-specific kill rates, and represent data from 1971 to 1998. Panel (c) is adapted from Vucetich and Peterson (2004b), depicts population-level kill rates, and represents data from 1971 to 2002

The extent to which such models are valuable is limited if the underlying relationships are inadequate. Below we inspect the inferences and attitudes arising from three efforts to analyze such models in the context of wolf management.

First, Messier (1994) conducted a graphical analysis of deterministic models of the functional and numerical responses. The parameters for these responses were based on data collected from 27 studies from across North America where wolves and their prey have been observed for five or fewer years. Messier (1994, p. 484) concludes, from this graphical analysis that

in the presence of a single predator, the wolf, moose would stabilize at ~ 1.3 moose/km², compared to an equilibrium density of 2.0 moose/km² with no predators” and that the addition of bear predation would reduce moose abundance to less than ~ 0.5 moose/km². Both [of these] equilibria are *caused* by density dependent food competition. If moose growth rate is reduced by only 5–10%, because of either a less productive habitat or a density invariant predation rate by an alternate predator like grizzly or black bear, a low density [< 0.5 moose/km²] equilibrium is predicted. This low equilibrium is the *result* of density dependent predation by wolves. The most striking feature of the model is the fact that a multiple-equilibrium system is practically impossible to generate [italics added].

We suppose it is the single-factor causal inferences (highlighted by the italicization) and/or the relative precision of the predictions that causes Messier (1994, p. 486) to ultimately conclude: “There is now a good theoretical and empirical understanding of the effect of wolf predation on moose population dynamics.”

Varley and Boyce (2006) conducted simulations to predict population dynamics of wolves and elk (*Cervus elaphus*) in Yellowstone National Park. Their simulations were based on stochastic functional and numerical responses derived from empirical considerations. Compared with Messier (1994), the modesty of their conclusions is striking (Varley and Boyce 2006, p. 331).

[Our] models consistently have predicted neither an insignificant effect of wolves on elk numbers as some had once believed, or enormous effects that are tantamount to ecological collapse as has been popularized outside the scientific community. Rather, the predictions are of moderate reductions in elk numbers with a sustainable, moderate hunter harvest.

They predicted that two very extreme cases are unlikely. Although one may be struck by the modesty of the inference, it is significant that the inference seems reasonably justified from the model.

Turchin’s (2003) analysis of a similarly structured model led him to be struck by that which most modelers of wolf populations had overlooked. Turchin (2003, p. 382) wrote

wherever deer populations are not heavily affected by humans, oscillations with a period of roughly 30–50 years appear to be the rule, rather than the exception. If cervid dynamics indeed turn out to be more prone to oscillation, then ... the current discourse about the limiting and regulating factors largely misses an important point... the main question becomes what factors are responsible for the oscillatory nature of dynamics, which factors ensure the oscillations do not get out of hand, and which factors are responsible for stochastic fluctuations in the realized per capita rate of change. (A partial answer to the last question, for moose on Isle Royale, is reflected in Fig. 3.4.)

Turchin may disagree (we are not sure), but his writing seems consistent with an important attitude expressed by Sir D’arcy Thompson, the so-called father of mathematical biology, and analyzed by the philosopher, E. Keller, in her book *Making Sense of Life* (Fox 2003). Thompson wrote, in his classic *On Growth and Form* (1942, p. 643) that “It is the principle involved, and not its ultimate and very complex results, that we can alone attempt to grapple with.” Although we may be able to understand and explain past dynamics, it seems overly optimistic to entertain even modestly precise predictions about future states of wolf and prey populations.

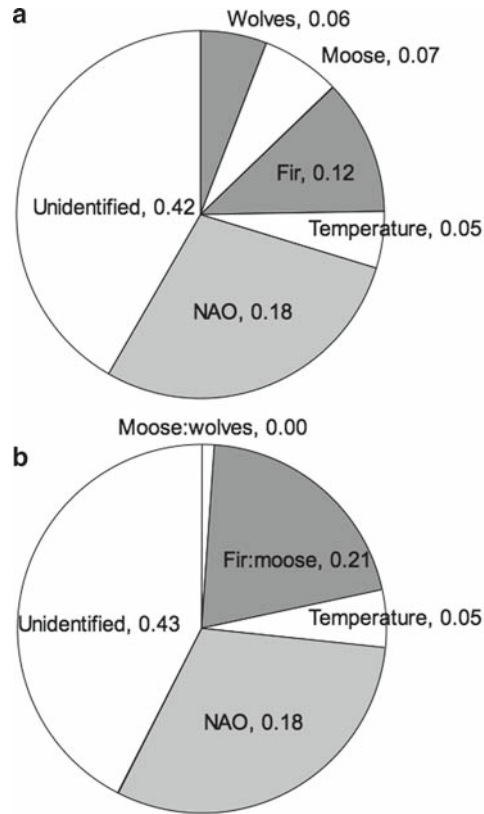


Fig. 3.4 The partitioning of variance for the growth rate of the moose population on Isle Royale (1959–2006) associated with two multiple regressions. Panel (a) relates growth rate to abundances, and panel (b) relates growth rate to ratios of abundances. Fir refers to balsam fir, the primary winter forage for moose; temperature is summer temperature; and NAO is the North-Atlantic Oscillation, which is an index of winter severity. Adapted from Vucetich and Peterson (2004b)

2. *Recruitment of moose is an important predictor of moose population growth, but it is not well predicted by the abundance of wolves.*

It is well established that wolves have a strong preference to prey upon calves relative to healthy, prime-aged ungulates (Peterson 1977; Wright et al. 2006). From this observation, some argue for wolf control because they believe that increased abundance of wolves reduces ungulate abundance (National Research Council 1997). However, preferring to prey on calves and reducing ungulate abundance are entirely different propositions. Observations from Isle Royale indicate that while calf recruitment *is* an important determinant of moose population growth rate (Fig. 3.5a), the rate of calf recruitment *is not* significantly impacted by the abundance of wolves (Fig. 3.5b). (On Isle Royale, calf recruitment is measured as the proportion

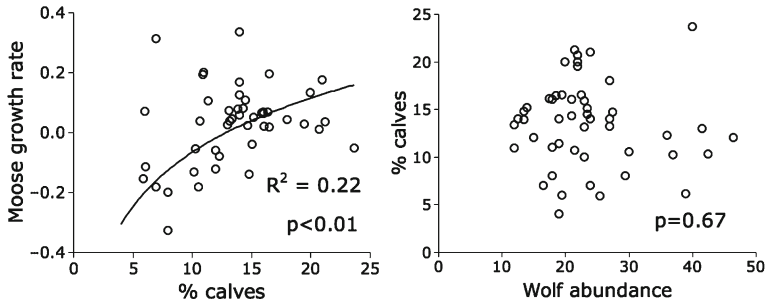


Fig. 3.5 Calf production has an important influence on growth rate of the moose population (*left panel*). However, the number of wolves is not well correlated with annual calf production (*right panel*). Percent calves is the percent of the total moose population in early February that are calves. Calf production depends on the combined effects of many factors (predation, food, and climate). The details are poorly understood. The number of wolves is the average of the current year and previous year. Data are from 1959 to 2007

of moose in the population that are calves during mid-winter.) Other evidence also lends support to the notion that fluctuations in wolf abundance do not necessarily impact the population growth rate of moose (Fig. 3.4), even though wolves prefer calves and calf recruitment has an important influence on moose population dynamics (Gaillard et al. 2000).

Two plausible explanations for the difference between the observations from Isle Royale and those of other studies, which suggest increased wolf abundance does reduce recruitment of ungulate prey (Gasaway et al. 1992; and references in Mech and Peterson 2003), are: (1) these other studies may be too short in duration to obtain an accurate perspective (see below) and (2) these studies also may be biased by a tendency to make observations when low recruitment happens to coincide with high wolf abundance, which does occasionally happen, even on Isle Royale (Fig. 3.5b).

3. *The relative influence of forage, predation, and climate on the population dynamics of moose on Isle Royale depends on the time scale.*

We recently analyzed data from Isle Royale with time series analyses to quantify the proportion of variation in moose population growth rate that could be attributed to annual fluctuations in predation (as indexed by wolf abundance), winter forage abundance (as indexed by dendrochronology of balsam fir and moose density), and climate (as indexed by the North Atlantic Oscillation). Using data observed between 1959 and 1999, that analysis indicated (Vucetich and Peterson 2004a) that (1) most fluctuations in moose population growth were not explained by any of these factors, (2) wolf abundance represented the least important factor, and (3) climate was more important than winter forage for explaining year-to-year fluctuations in the moose population (Fig. 3.4).

By contrast, alternative considerations were used to suggest that wolf predation represented a very strong top-down force on the moose of Isle Royale (McLaren and Peterson 1994). These considerations begin by observing that the accidental introduction of canine parvovirus to wolves on Isle Royale in 1980 represented a perturbation

that was exogenous to wolf–moose interactions. The disease triggered a nearly decade-long reduction in the abundance of wolves and was associated with a two- to threefold increase in abundance of moose over the same time period. Moose abundance was eventually reduced in 1996 by the convergence of three extreme events: the most severe winter of the twentieth century, a severe outbreak of winter ticks (*Dermacentor albipictus*), and a severe reduction in the abundance of forage.

These two analyses differ not only in their conclusion but also in the time scale being assessed. Whereas the regression analysis of Vucetich and Peterson (2004b) is primarily focused on short-term, year-to-year fluctuations in moose abundance, the historical analysis of McLaren and Peterson (1994) focused on a longer-term, decadal time scale. That is, McLaren and Peterson (1994) assessed how longer-term, sustained reduction in wolf abundance resulted in a decade long period of moose population growth.

More recently, we repeated the time series analyses described above on two subsets of the Isle Royale data, prior to and after the introduction of canine parvovirus. That analysis indicated that during the first two-decade period wolf abundance was the most important predictor of moose fluctuations, and that during the second two-decade period wolf predation was trivial in its importance, but climate was very important (Wilmers et al. 2006).

The most important lesson to derive from these analyses is that our sense about the relative strength of top–down, bottom–up, and abiotic factors can vary, even within a single system, with the time scale being considered and even the time period under consideration.

4. *Age structure of the moose population is an important predictor of wolf–moose dynamics.*

Relatively few models and predictions of ungulate population dynamics account for the influence of age structure. However, when it has been examined, the effect of age structure on ungulate population dynamics seemed to be important (e.g., Coulson et al. 2001; Festa-Bianchet et al. 2003). Age structure is an important element of population dynamics when several conditions hold: (1) age structure fluctuates over time, (2) such fluctuations are not entirely associated with other predictors of population growth (e.g., population density), and (3) population growth rate varies systematically with age structure. Moose on Isle Royale seem to be characterized by these conditions (Fig. 3.6).

It has long been known that wolves prefer to prey upon calves and senescent moose (Peterson 1977). However, it is not known to what extent varying age structure is caused by wolf predation (relative to, say, climatic variation) or the extent to which population dynamics of wolves are affected by variations in the age structure of their prey population. These underappreciated interactions likely account for important complexities in wolf–prey systems.

5. *The future dynamics of a managed population are as likely to be like past dynamics, as not.*

In the context of informal settings (e.g., public talks and discussions with managers and colleagues), we often characterize the most general conclusion of

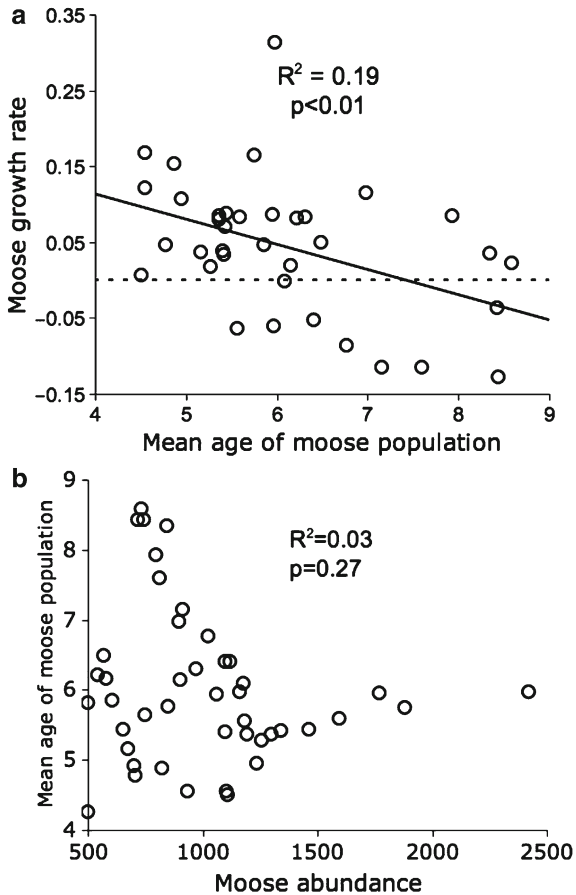


Fig. 3.6 The relationship between mean age of the population and population growth rate for moose on Isle Royale, 1959–1995 (a) and between moose abundance and mean age for the same time period (b). Mean age is derived from reconstructed population structure, which is based on necropsies of ~4,000 moose collected between 1958 and 2006. From the necropsies we learn the date of death and age at time of death. Data do not extend beyond 1995 because the reconstructed population structure cannot be estimated until most of the moose in a particular cohort are dead

research on wolves and moose on Isle Royale in two ways. First, even after 50 years of observation, each 5-year period of the wolf–moose chronology seems to be importantly different from every other 5-year period. Second, the longer we study, the more we realize how poorly we understand the population dynamics of wolves and moose on Isle Royale. We scrutinize these conclusions in formal analyses presented elsewhere (Vucetich et al. in press) and summarize the results of those analyses here.

- For no other purpose than as a heuristic, suppose that a simple explanation for a positive correlation between predator abundance and prey abundance is that

abundance of prey largely determines abundance of predators; a negative correlation may suggest that predators determine prey abundance and a weak correlation may indicate either a more complex interaction or a weak interaction. Between 1959 and 2006, the correlation between wolf abundance and moose abundance has been negative, but not strongly so ($r = -0.26$, $R^2 = 0.07$, $P = 0.08$). However, estimated correlations for shorter time intervals 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 5-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 Fig. 3.7.

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. 3.7a). 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. 3.7b). Keep in mind that R^2 is sometimes taken as a measure of the explanatory power of a model.

Studies of shorter duration (5–10 years) frequently suggest that simple explanations may provide high levels of predictive or explanatory power. However, studies of longer duration (>15 years) make clear that such simple explanations are of less value. Moreover, long-term research is also necessary for developing complex ideas. This is 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).

Even at the longest periods for which we can judge, wolf–moose dynamics from one time period differ from those of the previous time period. More precisely, the first 25-year period of wolf–moose dynamics was characterized by significantly stronger top–down influences than the second 25-year period of observation (Wilmers et al. 2006). It seems more likely than not that during the next 50 years wolf–moose dynamics will be different than they have been for the previous 50 years. Models that provided useful explanations of past dynamics were, as it turned out, a poor basis for inferring future dynamics, at least on Isle Royale. It seems reasonable to presume that this pattern would characterize many natural systems.

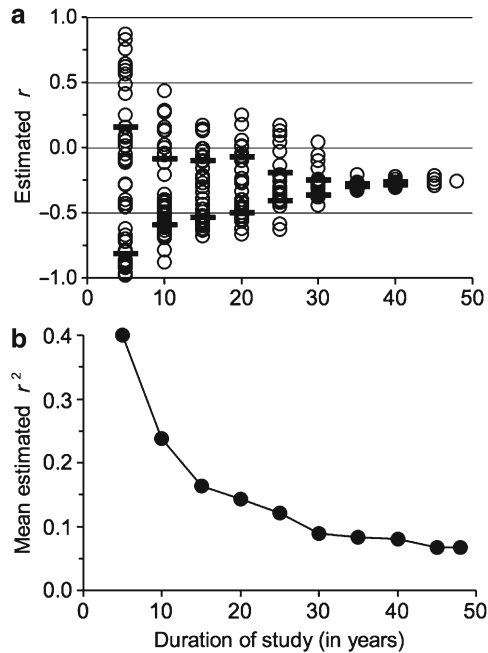


Fig. 3.7 **a** Estimated correlation coefficient (r) between abundance of wolves and abundance of moose across years (see Fig. 3.2). Each estimate is based on a different subset from the time series of abundances of wolves and moose. Each subset of data represents abundances from consequent years and 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 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. Adapted from Vucetich et al. (in press)

To distinguish good explanations of the past from reliable predictions of the future may have broad implications for conservation. Others have argued (e.g., Holling and Meffe 1996; Ludwig et al. 1993) that many conservation problems arise from our obsession for controlling and managing nature, an obsession fueled by a confident belief about our ability to control nature more reliably and precisely than may in fact be possible. An overconfident sense about one's ability to control nature is liable to arise from an overconfident sense about one's ability to predict natural phenomena, such as population growth rates. The Isle Royale experience suggests how overconfidence about our ability to predict nature may arise from confusing a model's ability to offer good explanations of the past with reliable and precise predictions of the future.

Students, managers, and members of the general public regularly ask us whether the limited ability to predict future dynamics of wolves and moose on Isle Royale

is occasion for discouragement about our effort to understand nature. Our reaction to such questions is that it seems we can be proud of the undeniably impressive knowledge we have about nature. However, it also remains true that our knowledge is pale when compared to nature's complexity. This juxtaposition – that we know much in an absolute sense, but very little in a relative sense – is not occasion for discouragement, but an occasion to be filled with wonder about and respect for the natural world. We find this attitude enriching, not discouraging.

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