TEMPORAL AND SPATIAL ASPECTS OF PREDATOR-PREY DYNAMICS

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ABSTRACT: Ungulates are both major consumers of vegetation and are themselves consumed by carnivores, so food web dynamics, both top-down (predation) and bottom-up (food and weather effects), are prominent in theoretical and applied research involving ungulates. The long generation time of ungulates induces long lags in population responses. Over broad geographic regions, ungulates commonly achieve high density only when predation is relatively low (< 2 species of predator), suggesting that predation provides a pervasive limitation of large herbivores. Ungulate stability is fundamentally a trophic-dynamics issue, usually a mix of top-down and bottom-up influences. The Isle Royale case history, spanning 4 decades, reveals a wolf-moose system fluctuating at 2-decade intervals with significant predation, food, and weather effects on ungulates. After a century, an equilibrium between moose and forest vegetation has not yet been reached, and a historical context seems necessary to understand trophic relationships. Components of predation compared at large spatial scales reveal different predator-prey patterns than the single system at Isle Royale, and analyses involving substitution of space for time also run counter to studies of single systems. Choice of spatial and temporal scales for field studies and meta-analyses appear to have a strong bearing on the results and their interpretation. Thus temporal and spatial scales enter influentially in the actual dynamics of carnivore-ungulate interaction as well problematically in our analyses of them.

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Interactions among trophic levels have been pervasive themes in animal ecology since its inception (Elton 1927). Ungulates are both major consumers of vegetation and are themselves consumed by carnivores, so studies of their population dynamics should reveal much about dominant trophic linkages in terrestrial systems (Schmitz et al. 2000). Ungulates are also large-bodied organisms; they may forage at local scales (Risenhoover 1987, Spalinger and Hobbs 1992), but they make decisions about movements that may cover tens or even hundreds of square kilometers. Their population dynamics and ecological influence may likewise reflect ecological phenomena that occur at different scales, e.g., vegetation patch dynamics and local nutrient fluxes may be tracked by foraging ungulates (White 1983, Pastor et al. 1997, Etzenhouser et al. 1998, Shipley et al. 1999), but their population dynamics may reflect broad-scale forest successional patterns or pervasive loss to predators with very large home ranges (Schwartz and Franzmann 1991, Gasaway et al. 1992). Their large body size also introduces potential complexity to predator-prey relationships. Ungulates may be larger than sympatric predators, thus difficult to kill as adults but more easily killed as slow-growing juveniles (Peterson 1977). Ungulates are relatively long-lived, with individuals persisting for many annual cycles of seasonal changes (Caughley and Krebs 1983), so ecological lag effects relating to maternal effects and individual vigor can be anticipated (Mech et al. 1991). Here we will attempt to assess how predator-prey dynamics, and our understanding of such dynamics, depends critically on several spatio-temporal scale issues, as illustrated by the wolf-moose-fir system at Isle Royale.

TOP-DOWN AND BOTTOM UP

The seminal essay by Hairston et al. (1960) provides a useful starting point for "modern" consideration of trophic linkages, by clearly laying out concepts that were spawned earlier by Elton (1927) and Lindemann (1942). Paine (1980) attached the name "trophic cascade" to the conceptual world of Hairston et al. (1960). Models by Rosenzweig (1968, 1969, 1971, 1973), Oksanen et al. (1981), and Oksanen (1983) furthered understanding of how length of food chains and variations in primary productivity might alter outcomes (Fretwell 1987). Opposing viewpoints were numerous, both then (Murdoch 1966, Ehrlich and Birch 1967) and now (Paine 2000, Polis et al. 2000, Schmitz et al. 2000).

For the most part, research on ungulate population dynamics has been a separate but parallel parade, highlighting the respective roles of density-dependence and predation (Krebs 1995). Ungulate researchers seemed "data-challenged", with findings limited by a paucity of experimental studies, the slow temporal scale of population fluctuations, and logistical challenges that have limited the spatial and temporal context of research. The search for general patterns in population ecology has not been spearheaded by large-mammal ecologists and, as a result, ungulate dynamics have usually been understood through a theoretical looking-glass that was built to view much smaller animals, even invertebrates (Eberhardt 1997). Or, more commonly, ungulate population dynamics were viewed in a game management context built around the dichotomy that populations were commonly limited by food or predators, with weather contributing to complexity (Bergerud 1980, Sinclair 1985, Mech et al. 1987, Fryxell and Sinclair 1988, Messier 1991, VanBallenberghe and Ballard 1994, Ballard and VanBallenberghe 1998). The food or predation dichotomy surfaces in the recent ecological literature as bottom-up or top-down control of food webs (Holt 2000, Power 2000), respectively, and may be generalized and enlarged into recent debate about ratio-dependent predation (Arditi and Ginzburg 1989) and trophic cascades (Paine 2000, Schmitz et al. 2000).

UNGULATES AND THEIR PREDATORS IN THE "REAL" WORLD

Several species of wild ursids, felids, and canids together consitute the predator fauna for Northern Hemisphere ungulates. By virtue of their widespread geographic distribution, group-hunting nature, and year-round activity, we argue that the gray wolf (*Canis lupus*) is the most significant predator of ungulates in the Northern Hemisphere. Where additional large predators coexist with wolves, along with human hunters, it is probably reasonable to assume that predation by these different species is at least partially additive, thus enlarging the ecological influence of carnivores.

It is also important to emphasize that humans continue to occupy an ecological niche as a top carnivore. As with other large predators, we have enormous potential to influence ungulate dynamics through additive mortality (Crête 1987), and certainly there is plenty of historical evidence that demonstrates our prowess in excluding other carnivores (Hampton 1997). Although we have instituted regulations to control our harvest, we have also increased in number ourselves and, through technology, we have greatly increased our ability to exploit and overexploit.

Two studies, on opposite sides of the North American continent, illustrate the significance of predation in an ecosystem context. Gasaway et al. (1992) compared moose (*Alces alces*) densities in 19 study areas in the Yukon and Alaska. The combination of wolf predation and bear (*Ursus* spp.) predation was sufficient to reduce moose to a level far below "ecological carrying capacity," where density-dependent responses to food shortage would be evident. This was true even in Denali National Park, where moose are not hunted by humans. Crête and Manseau (1996) contrasted predictions of prey-based trophic dynamics models (conforming to ideas of Hairston et al. 1960) with models relying on ratio-dependent predation, along a latitudinal productivity gradient (south to north) in the Québec-Labrador peninsula. Prey-based models predict that a change at one trophic level will prompt changes of alternating sign in successively lower trophic levels, while models of ratio-dependent predation predict that consumers and their resources will increase in parallel as ecosystem productivity increases (Arditi and Ginsburg 1989). Crête and Manseau (1996) found that tundra areas with inherently low productivity, where caribou (*Rangifer tarandus*) are the only ungulate present, supported a basic 2-link system (caribou and forage) and wolf predation was unimportant. Forage production increased within the forested zone where caribou and moose supported wolf populations, but both herbivores and carnivores were relatively scarce. Further south, just north of the Saint Lawrence River, forage production was high but predation by wolves and black bears (*Ursus americanus*) was thought to limit moose density. Where wolves were extirpated on the Gaspé Peninsula, moose were 7 times more abundant than in the wolf-inhabited area by the Saint Lawrence River, even though preferred-forage production was relatively low for that latitude. Results were interpreted as support for the so-called trophic-cascade model (Polis et al. 2000).

Gasaway et al. (1992) asserted that each additional large carnivore species resulted in a stepwise reduction in moose density. If one considers the wolf, brown bear, black bear, and human as the suite of potential predators of moose, we see a general pattern of reduced moose density with each additional predator, at least when large areas of contiguous habitat are considered (Fig. 1). Gasaway et al. (1992) compared moose density where predators were lightly exploited to those where preda-

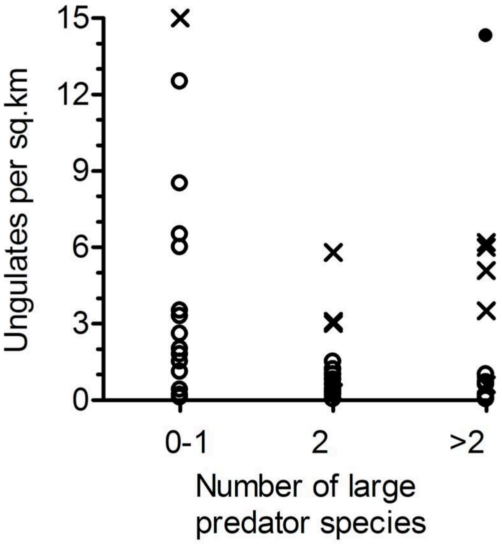

Fig. 1. Ungulate density is related to number of predator species in large areas of contiguous habitat where they are principal prey species for black bears, brown bears, gray wolves, and humans. Moose, elk, and bison are indicated by unfilled circles, white-tailed deer are indicated by "X", and elk in Yellowstone's Northern Range (prior to wolf introduction in 1995) are indicated by filled circle. Data points provided in Appendix 1.

tors were reduced by humans. The latter areas had an average moose density of 0.66 moose/km^2, while the former had 0.15 moose/km^2. Likewise, in the absence of predators, caribou exist at densities 2 orders of magnitude higher than when coexisting with multiple species of carnivore (Appendix 1). Caribou employ a spacing-out strategy to avoid wolf predation, and so exist at low density when coexisting with wolves (Bergerud 1983a, b).

Where moose coexist with only one predator species, they can achieve high population density (Fig. 1). Moose reach densities exceeding 2/km^2 in Sweden where they face only human hunters, now carefully regulated. In a park with no hunting on the Gaspé Peninsula in Québec, and only black bears as predators, moose density is also > 2/km^2. Moose exist at a comparably high density at Isle Royale, where unmanipulated wolves are the only predator.

Add a second predator species to any of these moose-dominated systems and one should expect a decline in moose density, a prediction borne out in many areas (Fig. 1). Put bears, wolves, and humans together in the same area, and only rarely would moose density exceed 1/km^2. With exceptionally favorable, but transient, habitat, moose reached 0.8/km^2 on Alaska's Kenai Peninsula, where a hunted moose population was also preyed on by wolves and black bears (Bangs and Bailey 1980, Peterson et al. 1984). But across the Northern Hemisphere, where moose are typically hunted by bears, wolves, and humans, their density is usually on the order of 0.4/km^2 or less.

Anything that increases the reproductive potential of a prey population will tend to reduce the impact of large carnivores (Seip 1995). Deer (*Odocoileus virginianus*), for example, should be able to coexist with wolves at a higher density than prey with lower rates of increase (e.g., caribou). Potentially, habitat improvement could accomplish the same (Orians et al. 1997). Thus, deer exist at higher density in north-central Minnesota, with intensive forest management, than in the old-growth forests of extreme northern Minnesota (Nelson and Mech 1986, Fuller 1989). Additionally, the presence of buffer prey may modify (increase or decrease) predation on a single prey species.

The mechanism by which predation limits ungulate populations is pervasive removal of pre-reproductive juveniles (Pimlott 1967); where juveniles survive poorly, populations tend to decline. At Isle Royale moose density increased during periods when calf overwinter survival was ~80%, but declined when survival was ~50% (R. Peterson, unpublished data). Predator reduction experiments improved moose calf survival about 3-fold and increased finite rate of population increase from 1.0 to 2.3 (Gasaway et al. 1992).

Over the past 25 years there have been numerous studies to determine the extent and nature of juvenile ungulate mortality (reviewed by Ballard and Larsen 1987**,** Van Ballenberghe 1987, Orians et al. 1997). In 11 studies located in 9 areas of Alaska, Yukon, and British Columbia where wolves and bears existed, radio-collars have been placed on 623 moose and 462 caribou soon after birth (Orians et al. 1997). Survival was monitored for variable periods, from 2 months to 1 year, but clearly there was an early period of greatest risk during the first 2 months of life. For both species, average (mean for all studies) survival rate of juveniles in their first year was only 40%. Ballard and Larsen **(**1987) and Van Ballenberghe **(**1987) cited several studies which indicated that predation on young moose may account for 79% of neonate deaths; survival in the first 8 weeks can be as low as 17%. Where moose were hunted in Alaska, losses to predation (31% of postcalving numbers) greatly exceeded loss to hunting (1.5%) and other losses (6%) (Gasaway et al. 1992). In an unhunted population free of bears and wolves (Rochester, Alberta), annual survival of moose calves was as high as 67%, and 41% of calf/cow groups in winter included twins (Rolley and Keith 1980).

Where 2 or more species of large carnivore were present (8 studies with 469 moose calves total), average survival to age of 6 months was 30%. In 3 study areas with 0-1 species of carnivore, average 6-months survival of moose was 67% (3 studies with 111 calves). Most mortality occurred within the first 6 weeks of life – black bears being responsible for 2-50%, grizzlies 3-52%, and wolves 2-18%. If moose density was high, approaching K carrying capacity, predator-induced mortality was considered more likely to be compensatory (Orians et al. 1997). Bear predation may be density-independent, but nevertheless a significant mortality factor in the first 6 months of life. On the other hand, wolf predation has its greatest impact in winter, when calves make up 30-40% of observed kills (Peterson 1977, Ballard et al. 1987, Mech et al. 1995). Page's (1989) analysis of cohort survival indicated that overwinter survival of moose calves ranged from only 30% to almost 100%, depending on wolf density and relative nutritional stress (caused by deep-snow winters and high population density).

Predation may likewise reduce adult survivorship (Van Ballenberghe and Ballard 1998), but variance in adult survival is much less than for juveniles. Adult survival rates depend heavily on the intensity of hunting. Peterson (1977) estimated that equilibrium survival of an unhunted moose population was ~87% for yearlings and adults; Gasaway et al. (1983) reported that the adult moose survival rate improved from 80% to 94% after wolf densities were reduced in the Tanana Flats, Alaska.

Messier (1994) reviewed 27 studies in which moose were the primary prey, and from his analysis he concluded that wolf predation was density-dependent at the low range of moose density, therefore regulatory. He predicted that moose would stabilize at 2 moose/km^2 in the absence of predators via density-dependent mechanisms, at 1.3 moose/km^2 in simple wolf/moose systems, and 0.2-0.4 moose/km^2 in a single stable-state (low density) equilibrium with multiple predators.

Thomas (1995) asserted that caribou have no intrinsic (e.g., social) population limitations. In his view the evolutionary pressure of wolf predation pervades caribou ecology. The suite of predators for caribou is dominated by wolves but also includes lynx (*Lynx canadensis*), coyote (*Canis latrans*), brown bear, black bear, cougar (*Felis concolor*), and wolverine (*Gulo gulo*). He stated that predators "can keep caribou populations depressed for long periods if alternate prey are abundant." Farnell and McDonald (1988) reported that recruitment of caribou increased 113% and adult mortality declined 60% in a population where wolf numbers were reduced 80%. Thomas (1995) concluded that when predators are present, average natural mortality of caribou is approximately 50% in calves in forest-tundra areas and 50-70% in forest-alpine and forest-forest moose zones; annual mortality was 7-30% in adults (Bergerud 1980, Farnell and McDonald 1988, Seip 1992). In contrast, annual mortality approaches zero where wolves are absent or rare. From his review of the literature, ranging from Kelsall (1968) to Seip (1992), Thomas (1995) concluded that (1) wolf predation is the major direct cause of natural mortality of calf and adult caribou and (2) dense caribou populations occur only in the absence of wolves.

From studies of deer in northern Minnesota, Mech et al. (1987) showed that deer fawn abundance was correlated not with wolf density but rather the cumulative severity of 3 previous winters. This does not indicate that wolves were unimportant in deer dynamics (cf. Mech and Karns 1977), but might instead mean that the dominant variance in the system was winter severity (Boyce and Anderson 1999). Further south in Minnesota, where timber harvest created optimum deer habitat, Fuller (1989) found that hunting mortality was more important than wolf predation in deer dynamics. Resource abundance may indeed modify the effect of predation through effects on reproduction and individual vigor.

WOLVES AND MOOSE ON ISLE ROYALE: DYNAMICS OF A SIMPLE SYSTEM

A perspective on wolf-moose relations in Isle Royale National Park (544-km^2 island in Lake Superior) is offered, to provide an update on a very dynamic case history and to illustrate temporal and spatial issues involved in interpreting predator-prey interactions. As moose and wolf populations have changed over the past 40 years (Fig. 2) there have been significant changes in how the system has been interpreted by observers, and valuable perspective has also been provided by studies elsewhere.

Annual winter counts of wolves began at Isle Royale about 10 years after the island was colonized by wolves in the late 1940s. Efforts were begun to estimate moose numbers, with methods steadily evolving into a "Gasaway-type" stratified plot count in which about 17% of the land area is intensively searched from aircraft in winter. An independent method to track historic change in moose numbers has been retrospective reconstruction, based on recoveries of approximately one-third of the moose after death (Page 1989).

Temporal Chronology

Early in the study, in the early 1960s, wolf population size was stable and moose exhibited a high twinning rate and also seemed relatively stable, so Mech (1966) suggested that wolf predation was keeping moose density (about 1/km^2) below the level at which food supply might be limiting. By the early 1970s, however, it was evident that moose had increased in the 1960s (Krefting 1974, Peterson 1977), reaching a level (almost 3/km^2) in the early 1970s where nutrition was poor, at least during severe winters in 1969-1972 (Peterson 1975). The wolf population expanded during 1969-1980 and moose density declined in 1972-1982 as wolf predation intensified. Wolves briefly reached in 1980 the highest year-round density documented for wolves in nature up to that time (almost 0.1/ km^2). As wolf numbers grew it was obvious that calf survival was negatively affected (Fig. 2), prompting population decline. Taking stock of the situation in the mid-1970s, Peterson (1977) interpreted the moose decline as a response to habitat deterioration as post-fire successional forests (regenerating after fires in 1936 and 1948) matured and moose became more dependent on older forests over 100 years old. Peterson (1977) asserted that density-dependent mechanisms prompted the moose decline, although wolf predation probably accelerated it. In short, wolf predation was considered largely compensatory, and not ultimately responsible for the moose decline. This was essentially a bottom-up interpretation, with the logical prediction being that moose density would stabilize at a new, lower level dictated by habitat, where it would remain as long as new forest disturbance did not intervene.

However, the moose population quickly grew again after the wolf population crashed in 1980-1982 (coincident with the arrival of canine parvovirus; Peterson et al. 1998). The 1981 cohort of moose calves, coincident with the wolf decline, was proportionately among the largest ever seen at Isle

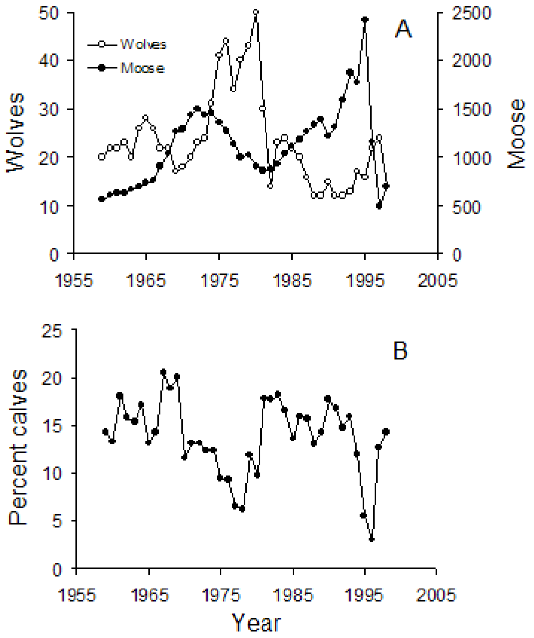

Fig. 2. Wolf population size and moose estimated population size, Isle Royale National Park, 1959-1998 (upper panel), and the proportion of calves (~6 months of age) in the moose population (lower panel). Each annual estimate of % calves is an average of a field-based estimate (mean of all available counts for each cohort, ranging from summer ground counts to aerial counts in autumn or winter) and an estimate based on population reconstruction (details at www.isleroyalewolf.org).

Royale, constituting about one-fifth of the moose population in mid-winter (Fig. 2). Peterson and Page (1983) acknowledged that wolf predation, not deficient habitat, had been limiting moose population growth – evidently predation loss was not simply compensatory. Significantly, balsam fir trees throughout the winter range of Isle Royale moose exhibited lagged oscillations in growth that mirrored the inverse of moose density – when wolves were high, moose declined, prompting growth of the forest (McLaren and Peterson 1994).

Throughout the 1980s and early 1990s, with low wolf numbers, the moose population grew almost without interruption (winter ticks were implicated in high mortality in 1989; DelGiudice et al. 1997). Wolves were themselves mysteriously maintained at a low level by lingering effects of disease, inbreeding, stochastic demography, or some combination of these factors (Peterson et al. 1998, Peterson 1999). By 1995 the moose population had grown to exceed 4/km^2 and there was ample evidence of severe undernutrition in winter. Twin calves were rarely seen, and moose phenotype reflected food shortage (Peterson 1995). Although calves were growth-retarded, most nevertheless survived their first winter to live on as adults; density-dependence was reflected in moose morphology but not in population dynamics.

The winter of 1995-1996 was the most extreme in a century (DelGiudice 1998, Post et al. 1999), with early winter storms, persistent deep snowcover, and cold temperatures that delayed the arrival of spring by about 6 weeks. Moose began dying of starvation by February 1996 and about 80% of the population perished in the next 3 months, reducing moose density once again to about 1/km^2. A dieoff of this scale also happened on Isle Royale in 1934, following the initial irruption of moose after colonization (Mech 1966).

Spatial Heterogeneity

While temporal variation in the Isle Royale chronology is striking, there is also spatial heterogeneity in this ecosystem. The east end of the island, by virtue of its glacial history, has thin soils and more forest disturbance caused by wind, resulting in more light reaching the forest floor (McLaren and Janke 1996). The resulting higher production of moose forage at the east end contrasts with conditions at the west end, where deep soils support old and tall deciduous forests that heavily shade the forest floor (Fig. 3). Balsam fir (*Abies balsamea*), a key winter forage species for moose

(Risenhoover 1987) is regenerating at high density at the east end but not at the west end. Somewhat paradoxically, this browse species receives proportionately less damage by moose herbivory in the thin soils at the east end of the island (McLaren 1996).

We used dendrochronology to determine the pattern of fir growth as a key component of the Isle Royale trophic system. Fir saplings and small trees growing with minimum competition for light were sampled from the west and east ends of the island. For each individual stem, ring widths were measured in cross-sections from the base of the stem. Each ring-width series was indexed following the method described in Chouinard and Filion (2001). Heights of fir stems on the west end ranged from 90-200 cm, while on the east end heights were 200-600 cm. All trees we sampled were from sites previously studied by McLaren and Peterson (1994).

Tree-ring growth, which may index abundance of fir forage, differs substantially across different portions of Isle Royale in some years (Fig. 3a). Spatial variation in fir growth may be the most significant aspect of spatial heterogeneity in the vegetation-moose-wolf system on Isle Royale. Is spatial heterogeneity in balsam fir manifested in the dynamics of higher trophic levels? To gain a preliminary understanding for how spatial variation in fir could be manifest in moose population dynamics, we consider how calf production is influenced by the abundance of fir forage. Using our data (Figs. 2 and 3a) and multiple linear regression we obtained the following model:

$$C_t = 0.15 - 3.3\times10^{-5}M_{t-1} + 4.6\times10^{-2}F_{t-1}, \quad (1)$$

where percent calf production in the current year (C_t) is dependent on moose abundance (M) and fir tree-ring index (F) in the previous year. For this model F_{t-1}, represents tree ring growth, averaged across all of Isle Royale. The coefficients for moose ($P = 0.03$) and fir ($P = 0.03$) are statistically

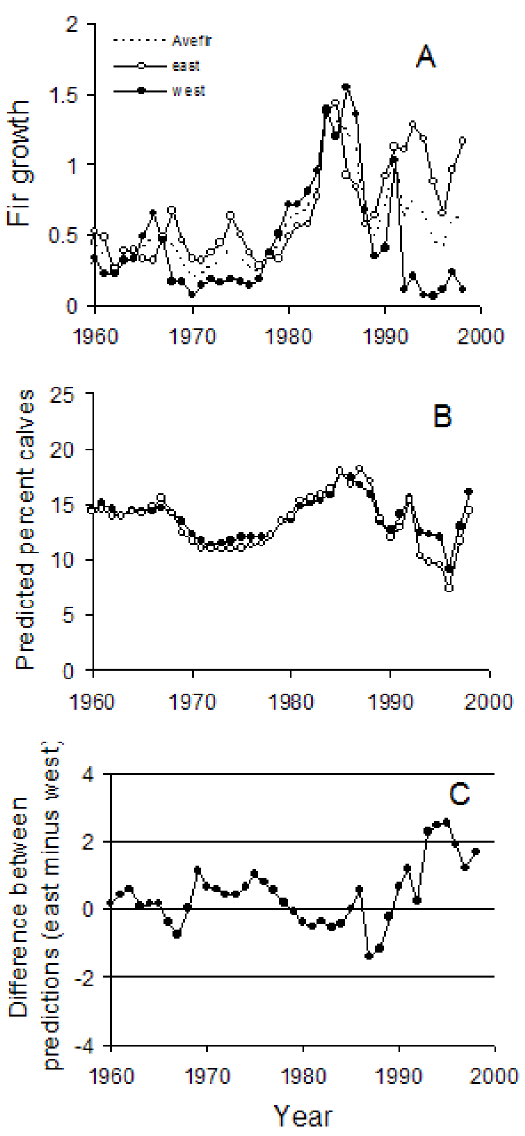

Fig. 3. Upper panel: Index of fir growth (see text) for eight trees located on the east half of Isle Royale and for eight trees located on the west half of Isle Royale. Middle panel: Two predictions of percent calves based on Equation (1) and the hypothetical assumptions that island-wide fir growth is characterized by fir growth that actually characterizes only the east half of the island (open circles) and only the west half of the island (closed circles). Lower panel: The difference between the two predicted percent calf

significant, and this model explains approximately 20% of the variation in calf production. The residuals of this model do not appear to deviate substantially from normal (P = 0.83), nor do they appear to be autocorrelated (Durbin-Watson statistic = 0.93). For this model, interannual variation in tree ring growth accounts for approximately 10% of the variation in calf production.

Consider, hypothetically, what the temporal dynamics of calf production would be like if fir growth across the entire island were like it has been on just the west end of Isle Royale, or just the east end of Isle Royale. To explore this hypothetical scenario, we predicted 2 time series of percent calf production using equation (1), except that for one time series we replaced $F_{t\text{-}1}$ with a series of values representing growth at the west end of Isle Royale, and for the other series, we replaced $F_{t\text{-}1}$ with a series of values representing growth at the east end of Isle Royale. These predicted percent calf time series are depicted in Figure 3b, and the absolute difference between these time series is depicted in Figure 3c. In absolute terms the difference between the two time series appears minor. However, the differences are highly autocorrelated. For example, for 11 consecutive years (1968-78) and for 9 consecutive years (1990-98) the difference is positive. Such a pattern could lead to substantial differences in moose population abundance. Investigation beyond the scope of this manuscript is required to accurately understand the extent to which spatial heterogeneity in fir could give rise to biologically significant spatial heterogeneity in moose population dynamics. Nevertheless, our hypothetical example suggests that further investigation could reveal important insights.

A convincing example of the importance of spatial differences in habitat emerged as moose population levels at opposite ends of Isle Royale diverged as a result of the moose die-off in 1996 when many moose survived in the thick fir stands at the east end but perished at the west end (R. O. Peterson and J. A. Vucetich, unpublished data). By 1999, 20 of the 25 wolves present were also supported by moose at the east end, so the bottom-up pulse of productivity was manifest at all 3 trophic levels. Thus, a long-term and large-scale pattern of soil development established as glaciers retreated was manifested in a rather peculiar historic fashion as a once-per-century severe winter impacted a moose population poised at a historic high population density. This example of the influence of spatial heterogeneity in fir dynamics highlights the need for an improved understanding of meso-scale spatial heterogeneity in wolf-ungulate dynamics across North America (cf. Orians et al. 1997).

WHAT'S SCALE GOT TO DO WITH IT?

With data on Isle Royale wolves and moose from any single 5-year period of the last 40 years, it would be possible to support almost any interpretation of their interaction, not unlike the fabled 10 blind men describing an elephant. Thus varying interpretations of predator-prey dynamics on Isle Royale (VanBallenberghe 1987) arose in part from the slow rate of change as a system initially interpreted as being in equilibrium (Mech 1966, Peterson 1977) has since exhibited long-term oscillatory tendencies (Peterson et al. 1984, McLaren and Peterson 1994). Different ecological factors have prevailed at different times. Temporal fluctuations at decadal intervals may be the norm for large-bodied ungulates and their prey, but this is much longer than our usual framework for research and management.

The dilemma of scale-dependent understanding appears to be a general one for animal ecology. Temporal and spatial variation in population density are not well-understood (in relation to environment), both for ungulates and other animals in general, but these lie at the core of our understanding of population regulation (Lundberg et al. 2000). Mechanisms underlying population variability will be elucidated only if appropriate response variables are studied at appropriate scales (Schmitz et al. 2000). Long response times may induce long lags; ungulate dynamics are drawn-out over decades, and response times for woody vegetation are even longer (Holt 2000).

The scale of study impacts interpretation of trophic interactions as well as dynamics of single-species populations (Wiens 1989). The Isle Royale case history provides a particularly compelling case for temporal variation in predator-prey interaction, which can now be anticipated for any regularly fluctuating system (Sinclair et al. 2000).

Comparisons of wolf and moose status over geographical scales may not always provide mechanistic insight into predator-prey dynamics. For example, a "global" correlation between average wolf and prey density exists over a wide range of prey densities (Fuller 1989). This is widely interpreted as the "numerical response" of the wolf to fluctuations in prey density (Messier 1994), even as an indication of ratio-dependent predation (Arditi et al. 1991), but the temporal trajectory followed by local populations conforms poorly to that which is extrapolated from the large spatial (but temporally static) global pattern. The long lives and long lags of large mammals may contribute to the poor match. What happens to the validity of models (Messier 1994) and management programs (Gasaway et al. 1983) when we ignore (lag-induced) temporal dynamics?

Large-scale geographic comparisons that ignore all temporal dynamics have also been used to assess predator-prey models of temporal dynamics. In a study from Québec (Crête and Manseau 1996), spatial patterns were used to support prey-dependent models of predation (sensu, Hairston et al. 1960) and to reject ratio-dependent models of predation (sensu, Arditi and Ginzburg 1989). However, it seems dubious to infer processes that occur in one dimension (time) from observations made in another dimension (space) (e.g., see also Abrams 1994, Lundberg and Fryxell 1995, Abrams and Ginzburg 2000). In fact, our analysis of the temporal dynamics of Isle Royale wolves and moose appear to support ratio-dependent predation (Vucetich et al. 2002).

The ecology of moose at Isle Royale includes both slow and fast ecological processes, operating at large and small spatial scales. Moose have virtually eliminated some plant species from the forest (e.g., *Taxus*), and intensive foraging may eliminate regeneration of many species (e.g., *Abies*) in the tree layer. Mesoscale dynamics are dominated by cyclical fluctuations in moose and wolves with a duration of about 2 decades, a product ultimately of generation time for predator and prey. Yet the forest itself has not equilibrated following the arrival of moose a century ago – at the island's west end old fir trees that established in the canopy before moose arrived are now dying of old age without replacement, and at the east end spruce-fir stands have only recently emerged in extensive 19th century burns initiated by mineral prospectors – while both trends are superficially associated with less forage for moose, future dynamics of wolves and moose in response to these very slow changes in vegetation are not readily predicted.

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Appendix 1. Data used in Figure 1.

Location	Species	Density/ km^2	Wolf	Human	Black bear	Brown bear	No. pred.	Deer-eq. dens.	Reference
Slate Islands	Caribou	6	0	0	0	0	0	12	Seip (1991)
Norway	Caribou	3.5	0	1	0	0	1	7	Seip (1991)
Newfoundland	Caribou	8.5	0	1	0	0	1	17	Seip (1991)
South Georgia	Caribou	2	0	1	0	0	1	4	Seip (1991)
Quesnel Lake	Caribou	0.03	1	0	1	0	2	0.06	Seip (1991)
Ontario	Caribou	0.03	1	1	1	0	3	0.06	Seip (1991)
Saskatchewan	Caribou	0.03	1	1	1	0	3	0.06	Seip (1991)
S. Finland	Moose	0.4	0	1	0	0	1	2.4	Nygren (1987)
Alberta	Moose	0.8	0	1	1	0	2	4.8	Rolley and Keith (1980)
Sweden	Moose	1.5	0	1	0	0	1	9	Cederlund and Markgren (1987)
Elk Island, Alberta	Moose	1.5	0	1	0	0	1	9	Cairns and Telfer (1980)
Newfoundland	Moose	1.8	0	1	0	0	1	10.8	Bergerud and Manuel (1968), Mercer and Manuel (1974), Fryxell et al. (1988)
Seward Pen, AK	Moose	0.4	0	1	0	1	2	2.4	Gasaway et al. (1992)
Riding Mt, Manitoba	Moose	0.8	1	1	0	0	2	4.8	Carbyn (1983)
Hecla Island, Manitoba	Moose	1	1	1	0	0	2	6	Crichton (1977)
Gaspesie, Quebec	Moose	2	0	0	1	0	1	12	Crête (1989)
Isle Royale, MI	Moose	2	1	0	0	0	1	12	Peterson (1999)
Aishihik, Yukon	Moose	0.1	1	1	0	1	3	0.6	Larsen (1982)
Kluane L., Yukon	Moose	0.1	1	1	1	1	4	0.6	Larsen (1982)
Denali, Alaska	Moose	0.2	1	0	0	1	2	1.2	Singer and Dalle-Molle (1985)
Nelchina Basin, AK	Moose	1	1	1	0	1	3	6	Gasaway et al. (1992)
Kenai Pen, AK	Moose	1.1	1	1	1	1	4	6.6	Bailey (1978), Peterson et al. (1984), Schwartz and Franzmann (1991)
S. Quebec	Moose	0.6	1	0	1	0	2	3.6	Potvin (1988)
Riding Mt, Manitoba	Moose	0.8	1	0	1	0	2	4.8	Carbyn (1983)
S. Central Ontario	Moose	0.3	1	0	1	0	2	1.8	Bergerud et al. (1983)
SW Quebec	Moose	0.3	1	0	1	0	2	1.8	Messier and Crête (1985)

...continued Appendix 1. Data used in Figure 1.

Location	Species	Density/ km^2	Wolf	Human	Black bear	Brown bear	No. pred.	Deer-eq. dens.	Reference
N. Alberta	Moose	0.2	1	1	1	0	3	1.2	Oosenbrug and Carbyn (1985)
NE Alberta	Moose	0.2	1	1	1	0	3	1.2	Fuller and Keith (1980)
GMU20A-AK	Moose	0.2	1	1	0	1	3	1.2	Gasaway et al. (1983)
Denali, Alaska	Moose	0.2	1	0	0	0	1	1.2	Haber (1977)
NE MN	Moose	0.6	1	1	1	0	3	3.6	Mech and Frenzel (1971), Peek et al. (1976), Nelson and Mech (1986)
N E MN	Moose	0.7	1	1	1	0	3	4.2	Van Ballenberghe et al. (1975)
E. Central Ontario	Moose	0.2	1	0	1	0	2	1.2	Pimlott et al. (1969)
E. Central Ontario	Wtdeer	3.1	1	0	1	0	2	3.1	Pimlott et al. (1969)
S. Quebec	Wtdeer	3	1	0	1	0	2	3	Potvin (1988)
E. Central Ontario	Wtdeer	5.8	1	0	1	0	2	5.8	Pimlott et al. (1969)
NE MN	Wtdeer	5.1	1	1	1	0	3	5.1	Van Ballenberghe et al. (1975)
N Central MN	Wtdeer	3.5	1	1	1	0	3	3.5	Stenlund (1955)
N Central MN	Wtdeer	6	1	1	1	0	3	6	Berg and Kuehn (1982)
N Central MN	Wtdeer	6.2	1	1	1	0	3	6.2	Fuller (1989)
Anticosti Island, PQ	Wtdeer	15	0	1	0	0	1	15	A. Chouinard (pers. commun.)
Riding Mt, Manitoba	Wtdeer	0.3	1	0	1	0	2	0.3	Carbyn (1983)
NE MN	Wtdeer	0.6	1	1	1	0	3	0.6	Mech (1986), Nelson and Mech (1986)
NE MN	Wtdeer	3.5	1	1	1	0	3	3.5	Mech and Frenzel (1971), Peek et al. (1976), Nelson and Mech (1986)
Wind Cave NP	Bison	2.6	0	1	0	0	1	20.8	Detling (1998)
Yellowstone NP	Elk	14.3	0	1	0	1	2	42.9	Singer et al. (1998a)
Rocky Mountain NP	Elk	12.5	0	1	0	0	1	37.5	Singer et al. (1998b)
Riding Mt, Manitoba	Elk	1.2	1	0	1	0	2	3.6	Carbyn (1983)
Wind Cave NP	Elk	3.3	0	1	0	0	1	9.9	Detling (1998)
Banff/Jasper NP	Elk	6.5	0	0	0	1	1	19.5	White et al. (1998)
Banff/Jasper NP	Elk	1.5	1	0	0	1	2	4.5	White et al. (1998)