Pages 281-292 in Biology and Conservation of Wild Canids, edited by D. Macdonald & C. Sillero-Zubiri, Oxford University Press.

CHAPTER 18

Grey wolves—Isle Royale

Long-term population and predation dynamics of wolves on Isle Royale

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Wolf *Canis lupus*, pack consumes a moose killed two days earlier in Isle Royale National park © R. O. Peterson.

The wolves (*Canis lupus*) of Isle Royale, an island (544 km^2) in Lake Superior (North America), have been studied with their primary prey, the moose (*Alces alces*), continuously and intensively since 1959. It is the longest study of such intensity in the world. The system is also importantly unique because on Isle Royale humans do not exploit wolves or moose, wolves are the only predator of moose, moose comprise an overwhelming majority of wolf prey, and the annual exchange of wolves and moose with the mainland is negligible. For this wolf–moose system, we present a chronology of research, general characteristics of the wolf population, and review some insights learned from studying the ecology of these wolves.

The wolves of Isle Royale

Chronology of wolves and wolf research on Isle Royale

Wolves first colonized Isle Royale National Park (Fig. 18.1) in the late 1940s—about 50 years after moose are thought to have first colonized the island. By 1930, moose probably exceeded 2000–3000 animals (4–6 moose/km^2; Peterson 1995b; see also Murie 1934). In 1934, a catastrophic, winter die-off reduced the moose population to a few hundred. In 1936, wildfire burned about 20% of the island, and subsequent moose population fluctuations during the next two decades were never documented. Another significant moose starvation event was

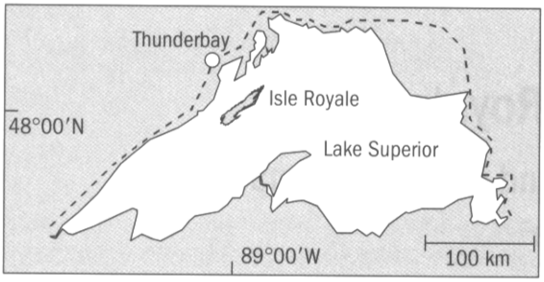

Figure 18.1 The location of Isle Royale National Park within Lake Superior, North America. The dotted line represents a highway.

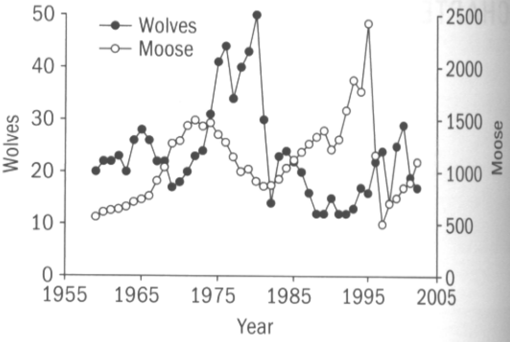

Figure 18.2 Population trajectories of wolves and moose on Isle Royale, 1959-2002. Each year the entire wolf population is counted from small aircraft (details in Peterson and Page 1988). The number of moose is estimated from aerial surveys (details in Peterson and Page 1993).

recorded in the late 1940s—about the time wolves arrived (Mech 1966).

Unable to stimulate federal sponsorship for Isle Royale wolf–moose research, Durward Allen moved and initiated what was envisioned to be a 10-year project in 1958 from Purdue University. During this 10-year period, Allen, graduate students, and post-doctoral investigators monitored wolf numbers annually, in addition to the ecology of moose, beaver (*Castor canadensis*), red fox (*Vulpes vulpes*), snowshoe hare (*Lepus americanus*), and deer mice (*Peromyscus maniculatus*) (Allen 1979). Long-term data sets, some extending back to 1959, now include wolf and moose population size, wolf social and spatial organization, wolf vital rates and predation rates, and characteristics of moose prey. These have been chronicled in a series of scientific and popular publications (Mech 1966; Jordan *et al.* 1967; Wolfe and Allen 1973; Peterson 1977; Allen 1979; Peterson and Page 1988; Peterson *et al.* 1998; Peterson 1995, 1999; Peterson and Vucetich 2001; Vucetich and Peterson 2002).

In addition, the ecology of lone wolves and small, non-territorial packs was reviewed by Thurber and Peterson (1993). Genetic characteristics of the wolf population were presented by Wayne *et al.* (1991) and Lehman *et al.* (1992). Evidence of occasional movement of wolves between the island and the mainland appears in Wolfe and Allen (1973) and Peterson (1979), but Wayne *et al.* (1991a) demonstrate that the entire wolf population in the late 1980s descended from a single maternal ancestor, probably the founding female.

In the late 1950s and early 1960s, wolves and moose both increased slowly (Fig. 18.2).

At the time, this relative stability was thought to characterize how the inclusion of predation led to a balance of nature (Allen and Mech 1963). During the late 1960s, the moose population nearly doubled from ~760 (1.4/km^2) to ~1400 (2.7/km^2). A series of winters with above average snowfall (1969–72) coincided with an end to rapid growth in the moose population. From 1969 to 1980, the wolf population nearly tripled from 17 to 50 wolves (from 31 to 92 wolves per 1000 km^2), during which time the moose population had risen, peaked, and began to fall again. Immediately after reaching this all-time peak, the population crashed in just 2 years to its lowest level ever, 14 wolves in 1982. These dramatic fluctuations inspire a very different interpretation of the balance of nature (Peterson 1995, 1999). The crash appears to have been caused by canine parvovirus, an infectious disease, and increased rates of wolves killing wolves in territorial disputes. Canine parvovirus was inadvertently introduced to Isle Royale by humans or their pet dogs, despite attempts to protect Isle Royale with the United States Wilderness Act (1963), which mandates 'wilderness to [be] affected primarily by the forces of nature, with the imprint of man's work substantially unnoticeable'. Since the crash, the number of wolves per moose has been substantially lower than before the crash, wolf extinction has at times seemed imminent, and the influence of inbreeding depression remains uncertain (Peterson *et al.* 1998). While wolves were at low density through the 1980s and early 1990s, the moose population increased to over 2000 animals (4 moose/km^2). Three-quarters of the moose starved to death in the severe winter of 1995–96, and aftershocks of this prey decline were seen in the wolf population through the close of the 1990s (Peterson and Vucetich 2001).

General characteristics of the Isle Royale wolf population

The wolf population is typically comprised of three or four packs. Each pack is typically comprised of 3–8 wolves, of which 2 or 3 are typically pups. In a typical year, one in six Isle Royale wolves lives as a loner or a member of a non-territorial pair. Although annual mortality rate varies substantially among years, one of every four or five wolves dies in a typical year (Fig. 18.3; Peterson *et al.* 1998). Two-thirds of all Isle Royale wolves die before the age of 5 years. Most deaths are probably associated with inter-pack strife or starvation. High and variable mortality rates are matched by similarly high and variable recruitment rates (Fig. 18.3; Peterson *et al.* 1998).

Associated with the high mortality rates is a dynamic social structure. On average, every 3 years one or more packs is dissolved, and usually replaced by a new pack in less than a year (Peterson and Page 1988; Peterson *et al.* 1998). For example, between 1980 and 1982, three old packs dissolved, and three new packs formed. Nevertheless, cases of long-term stability, such as a female wolf that led the west pack for 9 years (1987–95), also exist.

The Isle Royale packs are typically arranged linearly along the long axis of the island (Fig. 18.4). Wolves living in each of the pack territories experience vastly different densities of their primary prey, moose. Moose density at the east end of Isle Royale is typically twice that at the west end, and almost 10 times that of the middle third of Isle Royale (Fig. 18.4). Differences in moose density are attributable to differences in vegetation (Brander *et al.* 1990; McLaren and Janke 1996).

Depending on pack size and prey abundance, an Isle Royale wolf pack typically kills one moose every 4–10 days during winter (Thurber and Peterson 1993; Vucetich *et al.* 2002). Isle Royale wolves have some preference for killing calves and old moose (>9 yrs; Peterson 1977). Adult, wolf-killed moose frequently suffer from arthritis, jaw necrosis, or starvation (Peterson 1977). Depending on pack size and prey abundance, wolves may consume nearly all of a moose (including hide and bone marrow), or may consume only internal organs and some of the muscle tissue. Remaining tissue is typically consumed by scavenging foxes and ravens (*Corvus corax*).

The consequences of Isle Royale's isolation

Islands have long attracted the attention of evolutionary scientists (e.g. Wallace 1869; Kaneshiro 1988; Otte 1989; Roughgarden 1995; Sato *et al.* 2001). Case studies of island populations have also contributed importantly to understanding community ecology (Simberloff and Wilson 1969, Diamond 1975, Ricklefs and Bermingham 2001). Case studies of island populations, including the wolves and moose of Isle Royale,

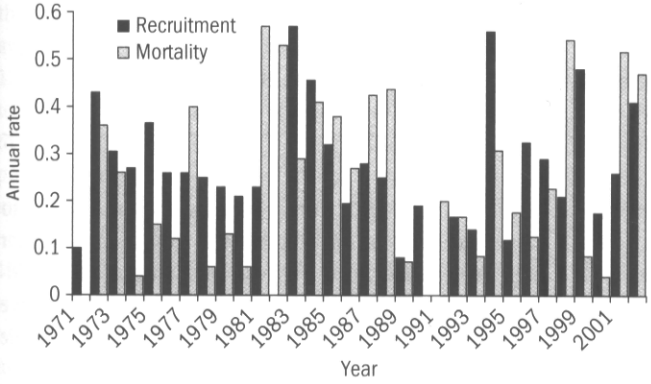

Figure 18.3 The annual rates of mortality and recruitment for the Isle Royale wolf population from 1971 to 2002 are relatively high and variable. The median mortality is 0.21 (interquartile range = (0.08, 0.40), coefficient of variation = 72%), and the median recruitment is 0.26 (interquartile range = (0.19, 0.32), coefficient of variation = 53%).

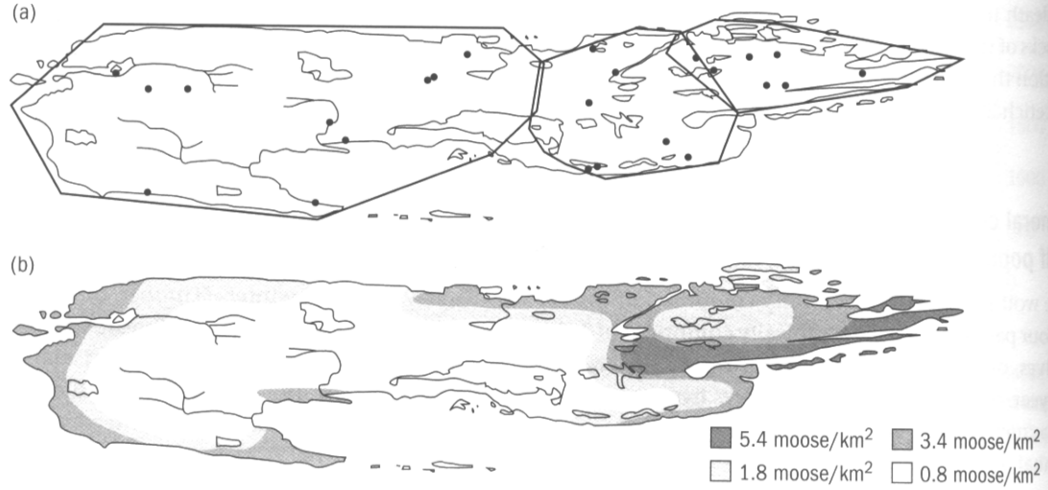

Figure 18.4 (a) Boundaries of the wolf packs on Isle Royale National Park in 2002. The dots represent the locations of moose kills made by each pack during a 6-week period in January and February of 2002. Winter kill rate data are based on these observations. In most years the population is comprised of three packs arranged along the long axis of the island. (b) Spatial variation in moose density on Isle Royale in 2002. Although absolute values change annually, the relative spatial pattern depicted here is representative of most years.

Table 18.1 Selected island case studies that have made distinctive contributions to various topics of population biology

Population regulation

Red deer on the Isle of Rhum (Albon *et al.* 2000), feral sheep of Soay Island (Coulson *et al.* 2001a), spiders on Gulf of California islands (Polis *et al.* 1998), community effects of predator removals (Terbough *et al.* 2001)

Predation

Wolf-moose interaction on Isle Royale (Vucetich *et al.* 2002), Mustelid-microtine interactions on islands in Fennoscandia (Heikkilae and Hanski 1994), fox-marten-hare interactions on islands in the northern Baltic (Marcstroem *et al.* 1989)

Competition

Arctic and snowshoe hare competition on islands off the coast of Newfoundland (Barta *et al.* 1989), Hermit crab competition on the San Juan Archipelago, Washington, USA (Abrams 1987), pararge butterfly competition on Madeira (Jones *et al.* 1998)

Extinction

Lizard populations in the Bahamas (Schoener *et al.* 2001), bird populations on islands off shore from Great Britain (Pimm *et al.* 1993; see also Vucetich *et al.* 2000), birds on Barro Colorado Island (Robinson 1999)

Population genetics

Sparrows of Mandarte Island (Keller 1998), *Peromyscus* on islands in inland lakes (e.g. Vucetich *et al.* 2001), finches of Galápagos (Grant and Grant 1992)

have also contributed uniquely to understanding several aspects of population biology (Table 18.1).

The value of the Isle Royale case study is importantly attributable to 25-km of open water (average annual temp ~4°C) that isolates Isle Royale from the mainland (Fig. 18.1). Although wolves would cross an ice bridge, they form only rarely, and access to the shoreline is limited by the town of Thunder Bay and a lakeshore highway. Because of this cold-water barrier, immigration and emigration have a negligible effect on demography of Isle Royale wolves and moose.

For most studies of demography, however, immigration and emigration represent substantial obstacles. When empirical observation is the basis for developing theory, the treatment of emigration and immigration often is *ad hoc* (e.g. Vucetich and Creel 1999), or heavily reliant on inference (e.g. Stacey and Taper 1992). Conversely, empirical validation of mechanistically based theory is limited by the estimation of emigration and immigration in real populations. Because the Isle Royale case study is unencumbered by these challenges, observations are more easily related to population biology theory (e.g. Vucetich *et al.* 1997; Eberhardt 1998).

The value of the Isle Royale case study is also facilitated by a synergy between observation and theory that is unencumbered by the complexity of ecological interactions associated with most other systems. Most generally, the species richness of Isle Royale mammals is only about one-third of that for nearby mainland areas. More specifically, potential prey such as white-tailed deer (*Odocoileus virginianus*) and potential competitors such as black bear (*Ursus americanus*) and coyote (*Canis latrans*) are absent from Isle Royale. Moreover, humans do not harvest either wolves or moose on Isle Royale. Thus, Isle Royale wolves and moose essentially represent a single-predator–single-prey system and can be adequately represented as a food chain. However, beaver is a minor component of summer diet for Isle Royale wolves (i.e. ~15%; Thurber and Peterson 1993). Elsewhere, wolves are embedded in substantially more complex food webs (see fig. 1 in Smith *et al.* 2003a; see also Polis and Strong 1996).

Another favourable property of the Isle Royale system is the number of individuals that comprise the populations of wolves and their prey. On average, Isle Royale is inhabited by 22 wolves and 1200 moose. At 544 km^2, Isle Royale is large enough to support a population of wolves, but small enough to permit complete annual censuses of the wolf population. Isle Royale is also small enough to permit annual surveys that include counting approximately 20% of the moose on Isle Royale (Peterson 1977). Our understanding of wolf–moose dynamics would be diminished, if Isle Royale were half or twice its size, or half or twice its distance from the mainland.

Summary of key contributions to science

Predation

Much predation research has focused on assessing how predation rates are affected by prey density, to the exclusion of other biotic and abiotic factors. This narrow scope reflects the canonization of early predation research that assessed only prey density, which seems to have slowed the acquisition of insights beyond those revealed by these early studies (e.g. Holling 1959; Rosenzweig and MacArthur 1963).

Research on wolves illustrates this historical interpretation of predation research. Most focus has been placed on the influence of prey density (e.g. Dale *et al.* 1994; Eberhardt 1998; Hayes and Harested 2000). However, despite vague appreciation that predation rates increase and carcass utilization decreases with deep snow cover (Nelson and Mech 1986; Fuller 1991; DelGiudice 1998), we have a poor understanding of how this important abiotic factor affects wolf–prey dynamics. Despite its potential importance, the effect of wolf density on predation rate is also poorly understood (Abrams and Ginzburg 2000; see also Yodzis 1994).

Since 1971, per capita kill rates (kills per wolf per month) have been estimated for a 45-day period each winter for each pack on Isle Royale. These observations indicate that estimated prey abundance on Isle Royale explains only 17% of the variation in the estimated per capita kill rates (Vucetich *et al.* 2002). However, a model that predicts kill rate from the ratio of prey to predators, a so-called ratio-dependent model (Akcakaya *et al.* 1995), explains 34% of the variation in kill rates, and outperformed models depending only on prey density as well as other models that depend on both predator and prey density (Vucetich *et al.* 2002). Also, a ratio-dependent kill rate model, modified to include the influence of seasonal snowfall, explains a total of 45% of the variation in per capita kill rate. Finally, when data from all packs each year are averaged, the per cent variation explained increases to 69% (Vucetich and Peterson unpublished result). Thus, an important component of variation in kill rates arises from variation among individual packs within a population (Fig. 18.5).

Figure 18.5 Wolf *Canis lupus*, pack in unsuccessful chase of moose, Isle Royale National Park © R. O. Peterson.

In contrast to our results, Messier (1994) reports that moose density explains 53% of the variation in per capita kill rates, and concludes that wolf predation is therefore a well-understood process. Several considerations suggest that this result and interpretation are misleading: (1) Messier's analysis is based on data from numerous short-term studies conducted across North America. Because spatial variation is not generally interchangeable with temporal variation, his analysis has limited relevance for temporal predation dynamics. (2) The explanatory power of Messier's analysis is artificially inflated because it relies heavily on data representing averages collected over several years from a single location. For example, Isle Royale is represented by 5 of the 14 data points in Messier's analysis. Each data point is an average of 5 years of data, and each year of data is an average of at least three packs. If these five data points were replaced by the >55 points that they represent, moose density would explain only 19% of the variation in kill rate. Although the inclusion of multiple observations from a single pack may represent pseudoreplication, this does not nullify the revelation that a substantial portion of variation in kill rate is unexplained and probably attributable to unexplained variation among packs within a population, and among years and within a single pack. Insights from Isle Royale suggest that wolf predation is more complex and less well-understood than has been suggested (cf. Messier 1994, p. 486).

Trophic cascades

Trophic cascades are the indirect effect of predator populations on plant populations, via direct influences on herbivore populations. Because the first well-documented trophic cascades were from marine (Paine 1966) and aquatic (Carpenter and Kitchell 1988) systems, and because of certain properties and assumptions of food chain models, trophic cascades are thought to be more common in aquatic systems than in terrestrial systems (Strong 1992; see also Chase 2000).

McLaren and Peterson (1994) reported that the dynamics of balsam fir (*Abies balsamea*) on Isle Royale were more closely linked to wolf–moose interactions than to seasonal weather patterns. This observation of predator dynamics impacting plant population dynamics was significant because such a pattern, manifest over several decades, had not been previously detected in a terrestrial system of long-lived vertebrates. Since then, numerous investigators have reported top-down effects in terrestrial ecosystems (reviewed by Schmitz *et al.* 2000; Chase 2000; see also Terbough *et al.* 2001).

Beyond assessing whether a community is or is not regulated by top-down processes, more recent trophic cascade research aims to: (1) compare the relative strengths of top-down and bottom-up processes (e.g. Polis *et al.* 1998); (2) assess top-down processes across different scales of space and time (Holt 2000; Power 2000); (3) understand the community characteristics that promote strong trophic cascades (Chase 2000); and (4) understand the relationship between the frequency of a trophic cascades and what portion of the community is affected (Polis *et al.* 2000).

A reassessment of the Isle Royale case study is needed to further understand (1) and (2). Preliminary re-analysis indicates that per capita rates of prey capture (a bottom-up process) explains only about 22% of the variation in wolf growth rate (Vucetich and Peterson in review). From the perspective of wolf growth rate, the rate of prey capture summarizes the influence of bottom-up processes. To the extent that this is true, top-down process on Isle Royale would appear very influential—perhaps 3–4 times more dominant that bottom-up processes ($(1-R^2)/R^2 = (1-0.22)/0.22 = 3.5$).

Another re-analysis indicates that substantially more variation in moose growth is explained by tree-ring growth of balsam fir (i.e. primary winter forage and a bottom-up process) than wolf abundance (i.e. the top-down process) (Vucetich and Peterson 2004). Importantly, weather variables explained more variation than did either of these biotic variables. Also, of the models examined, the most parsimonious explain only about half the variation in moose growth rate.

Multi-annual fluctuations

Populations, within and among taxa, exhibit a range of dynamical types: largely stable, eruptive, aperiodic multiannual fluctuations (MAF), and strong cycles with nearly constant periodicity. Population biologists have long been interested in understanding the mechanisms responsible for each dynamical type. The wolves and moose of Isle Royale clearly exhibit multiple consecutive years of increase, followed by multiple consecutive years of decrease (hereafter, MAF). These dynamics have been characterized as being cyclic (e.g. Peterson *et al.* 1984; McLaren and Peterson 1994; Post *et al.* 2002). This possibility is intriguing because most of our understanding of cycles is derived primarily from species with much smaller body size (e.g. hares, lemmings, *Synaptomys spp.*, and forest Lepidoptera) and much shorter cycle periods (10 years). However, it may be important to distinguish aperiodic MAF from MAF with nearly constant periods (hereafter, cycles). The distinction is important because the potential set of mechanisms that give rise to MAF may not be identical to those giving rise to cycles. If the Isle Royale system is cyclic, then the period is approximately 23 years, and we have observed approximately 1.8 cycles. This is hardly adequate for distinguishing between MAF and cycles.

Attempts to demonstrate cyclicity in the Isle Royale data distract from the value of assessing potential mechanisms that underlie the observed MAF. For example, the observed MAF may be the result of predator–prey *interactions*. If so, it would be important to discern whether observed MAF represent deterministic Lotka–Volterra processes, arising from destabilizing stochastic processes, or if they arise from a dynamic age structure of the moose population and wolves' limited ability to prey on prime-aged moose (3–9 years old).

In contrast to predator–prey interactions, moose might exhibit MAF independent of their interactions with wolves. Further, the MAF of wolves may arise merely as they track the fluctuating moose population. More specifically, moose MAF could represent delayed density dependence arising from intrinsic processes such as intraspecific competition or maternal effects (Berryman and Chen 1999; Keech *et al.* 2000). Alternatively, it is possible that MAF in moose arise from interactions with parasites, as has been considered for other vertebrate species (e.g. Moss and Watson 1995; Ives and Murray 1997).

Although assessing the constancy of the period in wolf–moose dynamics would be important, it seems unanswerable in the absence of a couple centuries of data or excessive reliance on inference. Fortunately, the pursuit of discerning the relative contributions of the above-mentioned processes would likely be feasible and profitable.

Foraging economics and the evolutionary maintenance of wolf sociality

Sociality is a conspicuous feature of wolves. A popular notion is that wolves live in large groups because it is required for capturing their usually large prey. However, observations from Isle Royale suggest that a single wolf can routinely capture moose, one of the largest species that wolves prey upon (Thurber and Peterson 1993). Nevertheless, group hunting may be favoured in wolves, like some other social species, because it confers increased foraging efficiency (Giraldeau and Caraco 2000). The positive relationship between average pack size and average prey size has been interpreted to support this claim (Nudds 1978; see Fig. 18.6). Observations from Isle Royale suggest that the per capita rate of prey capture decreases with pack size (Thurber and Peterson 1993; see also Schmidt and Mech 1997; Hayes *et al.* 2000). Such observations have been interpreted to mean that foraging economics do not favour sociality, and that kin selection is the sole selective force favouring sociality.

These ideas parallel the development of ideas related to understanding sociality in other large carnivores (e.g. Packer *et al.* 1990; Caro 1994; Creel and Creel 1995; Packer and Caro 1997). Unfortunately, most studies inadequately account for processes such as: (1) how foraging costs change with group size, (2) the instability of optimal group sizes (Giraldeau and Caraco 2000), and (3) per capita rates of food loss due to scavenging (by other species) for different group sizes. While some studies account for some of these factors (e.g. Carbone *et al.* 1997), no study to date has attempted to account for them all.

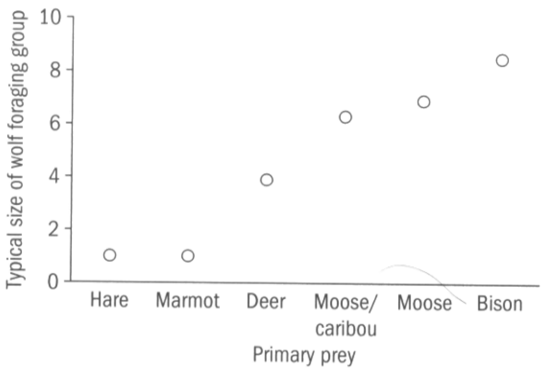

Figure 18.6 The relationship between prey type and size of wolf foraging group. Prey are ordered along the *x*-axis in order of size. Data are from Peterson *et al.* (1984), Carbyn *et al.* (1993), Messier (1994), Schmidt and Mech (1997), Hayes *et al.* (2000) and Schaller (2000) and represent averages for a study population or grand averages from several study populations. Although pack size tends to increase with prey size, variation in pack size for a given prey size is large. For example, pack sizes range from 2 to >20 for wolves that forage primarily moose and for wolves preying primarily on deer. Both increasing tendency and large variation are predicted by foraging theory based on rate maximization if the influence of raven scavenging is considered (Vucetich *et al.* 2004).

We recently used a combination of empirical observations and physiological modelling to estimate the net per capita rate of prey capture for Isle Royale wolves living in different-sized packs (Vucetich *et al.* 2004). This analysis suggests that the wolves living in larger packs capture less prey on a per capita basis than wolves in smaller packs. However, we also predicted the per capita rate of food loss due to scavenging for wolves living in different-sized packs. While feeding on a carcass, wolves may routinely lose 2–20 kg of prey per day to scavenging ravens. For rates of loss as low as 5 kg per day per moose carcass, the relationship between net rate of food intake and pack size is positive. Thus, large group size in wolves is favoured by social foraging benefits, because greater food-sharing costs in a larger pack are offset by smaller losses to scavengers.

Our analysis also indicates that because smaller prey are consumed faster, the rate of loss to scavengers is less, and wolves may afford to live in smaller packs when they forage on smaller prey. This is consistent with the observation that pack size tends to increase with prey size (Fig 18.6; see also Nudds 1978). However, our analysis also indicates that a wide range of pack sizes might form for any given prey size. This is consistent with observations that pack sizes for deer-killing wolves can be as large as 22 (Mech 2000a).

Kin selection certainly would seem to favour sociality in wolves (and other social carnivores). Another foraging theory, the resource dispersion hypothesis (see Macdonald *et al.*, Chapter 4, this volume), may also favour sociality in wolves. However, kin selection and the resource dispersion hypothesis do not appear to be the only selective force favouring sociality. Foraging economics also appears to favouring sociality among wolves, and perhaps other large, social carnivores.

Extinction risk and wolf sociality

Assessments of population viability and extinction risk have become a common pursuit in conservation research and a nearly ubiquitous component of managing endangered populations. An unresolved challenge seems to be assessing the accuracy and utility of analyses that are routinely limited by uncertainties in parameter estimates and model structure. Some conservation scientists seem optimistic about their value (e.g. Lindenmayer *et al.* 1993; Brook *et al.* 2000; see also www.cbsg.org/phvalist.htm), and others pessimistic (e.g. Beissinger and Westphal 1998; Ludwig 1999; White 2000). Evaluation of the accuracy and utility of viability assessments requires additional research to understand the consequences of ignoring potentially important processes or factors (e.g. age structure, density dependence, species interactions, and genetic processes).

Although most viability models ignore the influence of social structure, it may commonly affect population dynamics. The Isle Royale case study has been used to understand better how social structure affects extinction risk dynamics (Vucetich *et al.* 1997). Demographic data from the Isle Royale wolf population was used to construct a population viability model where each simulated wolf belonged to a pack and experienced age-specific mortality rates. The number of packs in the population depended on moose abundance, and recruitment was based on the number of packs in the population. The most important and general result of this analysis is that sociality may increase the population size required to eliminate demographic stochasticity as an important risk factor. The mechanism underlying this process is that the number of breeding units is equal to the number of packs, not the number of females. For example, the Isle Royale population has been small (e.g. 14 in 1982) and divided into just three packs, and much larger (e.g. 45 in 1976) but still comprised of the same number of breeding units (i.e. 3 packs). Since the publication of this chapter, further insights have been developed on how sociality and other behaviours affect extinction risk dynamics (e.g. Legendre *et al.* 1999; Reed 1999; Vucetich and Creel 1999; Courchamp *et al.* 2000; Courchamp and Macdonald 2001).

Evidence for inbreeding depression

Inbreeding depression is a decline in fitness due to inbreeding or genetic deterioration. Our understanding of inbreeding depression is based largely on theory (e.g. Vucetich and Waite 1999), laboratory experiments (e.g. Lacy *et al.* 1996), and captive zoo populations (e.g. Ballou 1997). Unfortunately, this understanding is limited by the simplifying assumptions that characterize theory and the artificial conditions that characterized laboratory and captive populations (e.g. Sheffer *et al.* 1997). Opportunities to examine inbreeding depression in unmanipulated populations (especially of vertebrate species) are rare and considered valuable (e.g. Wildt *et al.* 1987; Slate *et al.* 2000). The wolf population of Isle Royale has potential to provide insights on the nature of inbreeding depression. However, some obstacles prevent realizing any insights.

The Isle Royale wolf population was founded about 13 generations ago in the late 1940s by wolves that crossed an ice bridge connecting Isle Royale to the mainland (Mech 1966), and since has been completely isolated from the other wolf populations. Molecular studies suggest that all Isle Royale wolves have descended from a single female (Wayne *et al.* 1991). Demographic models indicate that the Isle Royale population has an effective population size (N_e) of approximately 3.8, and is expected to lose 13% (= $1/2N_e$) of its genetic diversity each generation (which is 4.2 years (Peterson *et al.* 1998)). This rate of inbreeding is comparable to repeated matings among first cousins. Molecular analyses of wolf genetic diversity corroborate these high rates of loss (Wayne *et al.* 1991). In 2002, the Isle Royale population was expected to have only ~18% of the founding population's diversity. Such rapid losses of large amounts of genetic diversity generally increase the risk of inbreeding depression (Ehiobu *et al.* 1989).

Direct evidence (i.e. Laikre and Ryman 1991) and indirect evidence (i.e. Smith *et al.* 1997) suggest that wolves are generally vulnerable to fitness loss in response to high rates of inbreeding. However, the potential for inbreeding to reduce fitness is highly variable among taxa (Crnokrak and Roff 1999) and among populations within a taxa (Lacy *et al.* 1996; Vucetich and Waite 1999). Wolves clearly illustrated this principle: Two captive, inbred populations of wolves have failed to show any fitness losses (Kalinowski *et al.* 1999). Nevertheless, these populations were less inbred, and the statistical power of analyses may have been weak (Kalinowski *et al.* 1999).

These general uncertainties about inbreeding depression limit assessments of inbreeding depression for Isle Royale wolves. Nevertheless, several observations are suggestive of inbreeding depression. For example, the number of wolves per moose greater than 9 years old has been substantially lower ever since the wolf population crash from 50 in 1980 to 12 in 1982 (5.7 ± 0.3 SE versus 18.2 ± 3.9; see also fig. 5 in Peterson *et al.* 1998). This could represent a manifestation of inbreeding depression via reduced abilities to capture prey or convert captured prey into wolf recruitment, or an overall reduction in wolf survival, independent of prey abundance. However, it remains unclear whether ecological processes alone can explain the reduced number of wolves per old moose.

In 2000, we recovered the skeleton of a dead wolf with two grossly asymmetrical vertebrae (Fig. 18.7). Although the deformities appear to be developmental abnormalities, it is unclear whether the deformity: (1) has a genetic or environmental basis, (2) occurs with greater frequency in the Isle Royale population than in non-inbred populations, and (3) led to reduced fitness. In 2003, we discovered a wolf carcass with its two middle toe pads fused in both front feet—a condition common in certain inbred breeds of domestic dog.

Successful studies of inbreeding depression in free-ranging populations are generally based on comparisons among populations (e.g. Wildt *et al.* 1987) or individuals (e.g. Slate *et al.* 2000) that exhibit varying levels of inbreeding. In the absence of such a comparison, inbreeding depression in free-ranging populations is difficult to assess. The greatest obstacle for such comparisons involving the Isle Royale population is eliminating the possibility that differences in fitness are attributable to ecological factors.

Contributions to conservation

The conservation and recovery of wolf populations is actively pursued in numerous regions of North America and Europe. Although conservation research is generally assumed to be an important component of successful conservation, this assumption is rarely scrutinized. In this section, we assess the possible influence of the Isle Royale case study on wolf conservation.

Since human-caused mortality has been a primary cause of endangerment or remains a potential threat, wolf conservation might be facilitated by better understanding the extent to which human-caused mortality is additive or compensatory with other causes of wolf mortality. Because little is known about this process, it may be useful to know that mortality rates in the Isle Royale wolf population, which has never been exploited, can be high and

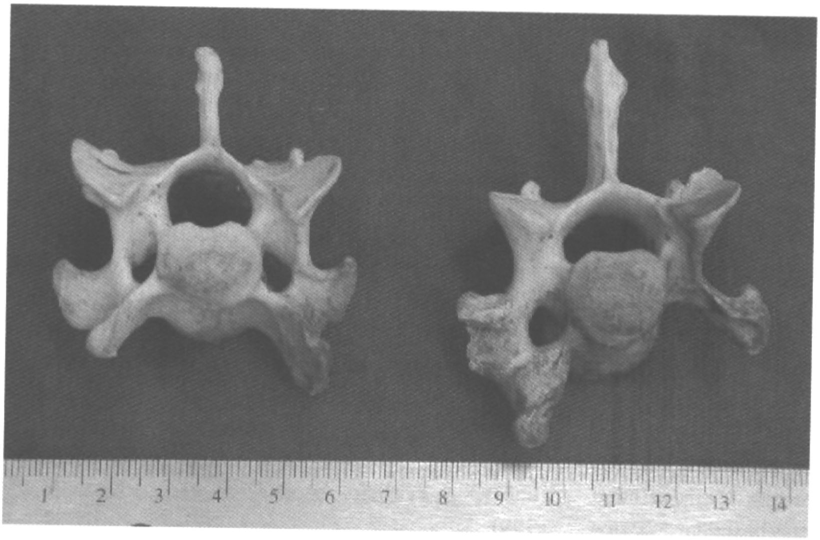

Figure 18.7 Gross asymmetry in a vertebrae from an Isle Royale wolf (#3529). This animal was born in the mid-1990s. Of the skeletal remains collected from approximately 35 Isle Royale wolves between 1959 and 2001, this is the only observed skeletal deformity. Nevertheless, the cause (environmental or genetic), frequency of occurrence, and fitness consequences of such deformities are unknown.

variable (Fig. 18.3). From this, one might infer that exploitation is not necessarily the cause of high and variable mortality rates in exploited wolf populations. Such an inference is, however, limited because Isle Royale may not be representative of unexploited wolf populations. Although this observation provides some perspective, its value for guiding conservation is limited.

Wolf conservation and recovery has also been concerned with understanding how many wolves and how large an area are required for population viability (e.g. Fritts and Carbyn 1995). The Isle Royale case study illustrates the possibility that a small, isolated population can persist, at least for several decades. This observation is also quite limited, because extinction and genetic drift are highly variable processes (Vucetich and Waite 1999), and a single case example may not be representative. Moreover, the requirements for long-term persistence are likely to differ from those for short-term persistence.

Wolf conservation is often justified by the notion that top predators, including wolves, are keystone species, and have a substantial influence on the ecosystems they inhabit. The Isle Royale case study provides a scientific basis for justifying this claim (McLaren and Peterson 1994) (Fig. 18.8).

Several issues have been critical to wolf conservation for which the Isle Royale case study has contributed little or no insight. These issues include: (1) taxonomic relationships among historical populations and recovering populations (e.g. Wilson *et al.* 2000), (2) biological details of how to translocate and release wolves into a new environment (e.g. hard and soft releases; see also van Manen *et al.* 2000), and (3) the amount of gene flow required to maintain natural population genetical processes (e.g. Forbes and Boyd 1997).

Perhaps the most important factor determining the success of wolf recovery and conservation has been the relationship between humans and wolves. The attitudes of North American humans towards wolves began to change in the late 1960s and early 1970s (Dunlap 1988). During this time, the Isle Royale case study was a prominent example to the general public of the value of wolves. *National Geographic* published *Wolves versus moose on Isle Royale* in its February 1963 issue, with a follow-up article in 1985 (i.e. Eliot 1985). Also during this time, two nationally broadcast films featured the Isle Royale case example (*Wolf Men* (1969) and *Death of a Legend* (1970)). The Isle Royale case study continues to heighten awareness of wolves for thousands of people through visitation to Isle Royale National Park, participation in EarthWatch expeditions (www.earthwatch.org/expeditions/peterson.html), wide distribution of annual reports, a popular book accounting the Isle Royale case study (Peterson 1995), and a web page (Vucetich and Peterson 2002).

The positive impact that Isle Royale wolves have had on the general public may also be reflected in the general public's interest in and support for wolf research on Isle Royale. National wire services

Figure 18.8 After killing a moose calf (*Alces alces*) in Isle Royale National Park, these two wolves (*Canis lupus*) successfully despatched the calf's mother. © R. O. Peterson.

consistently report the results of the annual wolf censuses on Isle Royale. Broad public support is also reflected in continuous financial support from a diverse array of non-governmental agencies and individuals, such as the National Rifle Association and Defenders of Wildlife. In fact, public interest alone forced Department of Interior officials to abandon an effort to scuttle the study in 1983 during the Reagan administration.

The Isle Royale case example may, however, also generate attitudes among the public that inadvertently hinder wolf recovery. First, the isolation and wilderness designation of Isle Royale probably contributes to the erroneous conception that wolves are restricted to wilderness areas far from where people live (cf. Haight *et al.* 1998; Mech 1995). This misconception may complicate the management of wolf–human conflicts. Second, the Isle Royale case study may also provide the general public with the idea that recovery of unexploited wolf populations will result in a 'balance of nature'. This is valuable, unless the general public does not appreciate that a 'balance of nature' may include periods of boom and bust for populations of both wolves and their prey.

An important, but difficult to quantify, contribution of the Isle Royale case study is professional training of people who have actively contributed to wolf conservation (and several of whom, are authors in this book). Specifically, D. Mech, whose PhD is based on the Isle Royale wolf population, has been a global leader in wolf conservation for four decades. R. Peterson also earned a PhD based on these wolves, and has contributed to the assessment and monitoring of wolf conservation in Alaska, the Great Lakes, and Scandinavia. D. W. Smith, studied the wolves of Isle Royale as a student for over a decade, and since 1996 has led the Yellowstone Wolf Project. M. K. Phillips was a field assistant for the Isle Royale wolf project in 1981, and has since directed reintroduction efforts of red wolves in North Carolina, and grey wolves in Yellowstone and the Southern Rocky Mountains. Finally, J. A. Vucetich began studying Isle Royale wolves in 1989, and has since contributed to monitoring and assessing wolf conservation in Michigan, in Algonquin Provincial Park, and for the Mexican Wolf Recovery Program.

The Isle Royale case study seems to have contributed to wolf conservation and recovery. However, the educational impact and inspiration of the Isle Royale story on the general public and researchers alike may have been more important than the scientific insight it has offered. Conservation scientists should consider the generality of this circumstance, and conduct their research with appropriate concern for its educational and inspirational impact on professionals, students, and the public.

Acknowledgements

Major support of these studies was received from the EarthWatch Institute, National Geographic Society, U.S. National Park Service, (DEB- and the U.S. National Science Foundation 9903671) plus numerous private donations. Any opinions, findings, and conclusions or recommendations expressed here are those of the authors and do not necessarily reflect the views of the National Science Foundation.