Discernment and Precaution: A Response to Cochrane and Mech

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Consider the following line of thinking. For islands that are small and isolated, extinction is an authentic element of their biological integrity. A critical purpose of a park is to protect biological integrity. From those two points it would be best to refrain from conserving wolf predation as an ecological process in Isle Royale National Park and allow Isle Royale wolves to go extinct—if that is what should come to pass. Furthermore, wolves and moose might never have existed on Isle Royale were it not for human actions. As such, Isle Royale wolves and moose might be exotic species. A critical purpose of a park is to minimize and mitigate against human influences, especially exotic species. Consequently, we should celebrate the extinction of wolves and moose from Isle Royale if they were to go extinct. This seems to be the line of thinking that underlies Cochrane's paper in this issue (Cochrane 2013). The soundness of this line of thinking can be evaluated with several considerations.

Yes, of course, Isle Royale is well characterized by its island nature—a condition where extinction is common. However, being prone to extinction is not what makes Isle Royale distinctive. Humans have made most of the planet's ecosystems prone to species extinction. What makes Isle Royale globally distinctive is being inhabited by an un-persecuted top predator, a large herbivore whose condition is not dominated by the influence of hunting, and a forest protected from commercial logging. Such landscapes used to be commonplace across the planet. Today, we have relegated these kinds of landscapes to small, isolated "islands" that are prone to extinction. It might be perverse to opt for extinction on Isle Royale, because extinction is a natural feature of islands, at the expense of actively conserving an example of biological integrity that was once commonplace but now profoundly rare because of widespread carnivore extinctions.[1]

The line of thinking underpinning Cochrane 2013 also depends on the belief that Isle Royale moose might be exotic species. That conclusion depends on wildly speculative evidence.[2] Moreover, there are no credible plans to remove moose from Isle Royale or harvest them with the intensity that would be required to replace the influence of wolf predation.[3] So long as moose are present, Isle Royale's biological integrity and ecosystem health depends vitally on the presence of wolf predation. Allowing for the extirpation of wolf predation and the harm to ecosystem health that would ensue seems a peculiar reaction to speculation that moose inhabit Isle Royale because people brought them.

Isle Royale wolves, an exotic species?

Cochrane (2013) also forwards several lines of thought intending to develop the belief that

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wolves are a kind of un-natural phenomenon on Isle Royale, that they are an exotic species, and that National Park Service policy would suggest that their loss should be encouraged and celebrated. In developing this belief, Cochrane observes, for example, the absence of archaeological evidence indicating the presence of wolves on Isle Royale between ca. 5000 BCE and the time when historic records become available (ca. 1750 CE). It is doubtful that wolves, very rare carnivores, would reliably appear in Isle Royale's archeological record. As such, that absence of evidence is not evidence of wolves' absence. Even in historic times, the presence of wolves cannot be reliably ruled out.[4]

Cochrane also speculates that captive-born wolves released by humans may have contributed to the gene pool of Isle Royale wolves. Even if that speculation were true,[5] it would not make Isle Royale wolves an exotic species—because wild-born wolves had colonized Isle Royale several years before.

Finally, Cochrane believes that wolves' arrival on Isle Royale in the mid-20th century is, in part, attributable to logging practices on the mainland that made wolves more abundant than would otherwise have been the case, which in turn increased their probability of colonization. Some discernment is required. Virtually every ecological event of conservation value has a causal chain tracing back to humans. To believe that every indirect effect of humans on nature is a blight on nature would be to think that essentially all of nature is blighted. Such an attitude is deeply misanthropic. It would be stunning to think that NPS policy would favor an absence of wolf predation on Isle Royale on the wild speculation that they are an exotic species or blighted because humans have influenced them.

Inbreeding depression

Mech (2013) defends the position that it would be best to refrain from conserving wolf predation on Isle Royale through genetic rescue. That conclusion seems based largely on two basic premises that could be expressed as: (1) Isle Royale wolves are unlikely to go extinct as a result of inbreeding depression, and (2) the scientific disciplines concerned with extinction risk and conservation genetics would benefit more from observing Isle Royale wolves in the absence of genetic rescue.

The first premise seems to depend, in part, on a line of reasoning roughly expressed as: (1) periods of low recruitment rate, such as that observed in recent years on Isle Royale, are not uncommon in wolf populations and are not evidence of elevated risk of extinction due to inbreeding depression; (2) limited ability to acquire food is a more plausible explanation for low recruitment; and (3) the recent period of food limitation on Isle Royale, like other such periods in the past, is expected to be temporary. This line of thinking seems at least weakened by observing that the rate at which wolves acquire food has been a poor predictor of recruitment rate for Isle Royale wolves (Marucco et al. 2012), and population growth rate has been lower than expected given the rate at which wolves acquire prey for each of the past five years (2008–2012).[6] A plausible explanation for those results is that inbreeding depression has had an important influence on recruitment in the Isle Royale population. Nevertheless, low rates of recruitment, *per se*, are not the primary evidence for thinking that inbreeding depression places Isle Royale wolves at considerable risk of extinction.

Mech (2013) also cites Ware and Holahan (2010) to doubt that "skeletal abnormalities are truly a result of inbreeding, however, because similar abnormalities have been found in other wolf populations on the mainland surrounding [Isle Royale]." That study has not been made available to us or recorded in an open venue where it can be evaluated. One concern is that the frequency of lumbosacral transitional vertebra (LSTV) in a population depends on the standards used to determine whether any particular specimen should be classified as exhibiting LSTV (Lappalainen et al 2012; Ondreka et al. 2013). Even if the high incidence of malformities in Isle Royale wolves were dismissed as evidence, the tendency for those malformities to have increased over time is very much indicative of inbreeding depression (Räikkönen et al. 2009).[7] Most importantly, if those malformations were overlooked entirely, the evidence that Isle Royale wolves have been exhibiting high rates of inbreeding and inbreeding depression is considerable (i.e., Adams et al. 2011).[8]

With respect to the second premise, a great deal is known about the negative effects of inbreeding depression on extinction. Expecting to gain additional significant knowledge by observing nuanced genetic details about the extinction of Isle Royale wolves would be like hoping to gain significant knowledge about the effects of diet on heart disease by observing the heart rate of a patient with heart disease in the last moments of his or her life.[9] By contrast, relatively little is known about how to most effectively implement genetic rescue, which is a potentially valuable tool for conserving many populations across the planet. Documenting the effects of genetic rescue on Isle Royale wolves would result in significant gains in knowledge on that subject.[10]

Other issues

We have highlighted that considerable scientific uncertainty exists about how climate change affects moose (e.g., Vucetich et al. 2013). In that regard we are in agreement with Mech (2013). While that uncertainty is relevant, it does not, to our understanding, support any argument against the value of conserving wolf predation on Isle Royale.

Mech (2013) concludes that evidence is "sparse" for thinking that canine parvovirus (CPV) has importantly influenced the population dynamics of Isle Royale wolves. One reason offered is that food shortage is a more plausible explanation for the 1980–1982 population decline. We do not doubt that food limitation played a role in that decline.[11] However, that observation is not evidence that CPV has been unimportant—multi-causality is a hallmark of ecological phenomena. Other reasons offered rely on the apparently limited effect that CPV had on one outbred population (e.g., Mech and Goyal 1995). Those reasons neglect to account for variation among populations in susceptibility to disease (e.g., Tobler and Schmidt 2010), and that variation can arise from a variety of causes, including being food stressed or severely inbred (e.g., Spielman et al. 2004). Mech (2013) raises other concerns about CPV that can also be refuted, but space does not permit us to do so here. Most importantly, if decisions about managing Isle Royale wolves depend on understanding the influence of CPV on Isle Royale, then that topic should be reviewed by a panel of disease specialists (see footnote 7). Any such review would have to address the concern that the two most significant population declines in the history of Isle Royale wolves (1980–1982 and 2009–2013) coincide with the only two periods in their history during which exposure to CPV has been detected.

Precautionary principle

We appreciate developing a decision about Isle Royale wolves that is mindful of scientific opportunity; however, concern for ecosystem health and biological integrity is very likely the more important foundation for this management decision.

With respect to concern for ecosystem health, it is relevant to ask, are Isle Royale wolves certain to go extinct in the next few years? No. Might they pull out of this period of low abundance in a scenario akin to that observed in the late 1990s?[12] Yes, it is possible. Many things are possible. Our concern is not for what is possible. Our concern is for what is likely[13] and for application of the precautionary principle. The problem with allowing wolves to go extinct and then reintroducing a new population is that that action would very likely be associated with a significant gap in predation on Isle Royale. This, in turn, would result in damage to Isle Royale's ecosystem that might be irreversible.

A gap in predation's influence has already begun, as the lowest predation rates ever observed on Isle Royale occurred in 2012 and 2013. The result has been a 70% increase in moose abundance. Increased moose abundance caused by low predation has the potential to cause considerable, long-standing harm to Isle Royale's ecosystem health.

Here is a brief summary of the details behind this concern. Throughout most of Isle Royale, where balsam fir trees live, those trees are either old canopy trees, established roughly a century ago at about the time moose first arrived to Isle Royale, or they are shorter than about 1.5 meters (Brandner et al. 1990). The short fir trees are important food for moose during winter and are kept short by moose browsing. Older canopy trees are the only source of seeds to regenerate the species. Because of their age, the canopy trees have been rapidly dying and will soon be functionally absent (Frelich et al. 2012).

Some small balsam fir trees might have had a chance to grow into the canopy in the 1980s. However, any such growth was prevented by dramatic increases in moose abundance that resulted from a crash in the wolf population. That crash was likely caused and exacerbated by a wolf disease that humans inadvertently introduced.

However, the moose population recently (2005–2011) experienced the most protracted period of low abundance ever observed. That low abundance was, in part, attributable to predation. During that period, the shorter fir trees began growing at an unprecedented rate. By 2013, many were approaching a height (>3 meters) where they will both begin to produce seeds and grow into the canopy. This potential growth into the canopy is an event that has not occurred in more than a century, and it is much less likely to occur if predation rates remain functionally absent for any significant period of time. Discontinuity in predation is significant because restoring predation after its absence does not necessarily restore an ecosystem (e.g., Schmitz 2004). For example, the absence of wolf predation in Yellowstone allowed elk to outcompete beavers, greatly reducing the abundance of willow and beaver. The resulting alterations to hydrology appear to be not readily reversible, even after restoration of wolves (Marshall et al. 2013).[14] That pervasive influence of top predators means a discontinuity in predation is likely to have unanticipated negative effects on ecosystem health (Terborgh and Estes 2010).

Mech (2013) states that "concerns [about ecosystem health] are premature at this time because [Isle Royale National Park] still harbors a functioning wolf population that could

well persist for many years with or without human intervention." Our concern is that the functional loss of wolf predation began two winters ago in January 2012 when predation rates hit record-low levels and may not return unless active conservation measures are taken. The watchful waiting suggested in Mech (2013) is associated with considerable risk of long-lasting damage to Isle Royale's ecosystem health.

Mech (2013) also states that whether the "effects [of top predators] are positive or negative is a matter of judgment." We agree. It happens to be the judgment of luminaries such as Aldo Leopold, whose view is aptly captured by his oft-repeated aphorisms, "To keep every cog and wheel is the first precaution of intelligent tinkering" and "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise." Finally, if an aspect of nature is valued, it seems more appropriate to conserve it rather than to let it be lost with the hope that it can later be restored. For these reasons associated with the precautionary principle, genetic rescue appears to be the most appropriate response.

Endnotes

1. Circumstances on Isle Royale may be globally unique. We are unaware of any other place on the planet inhabited by an un-persecuted top predator, a large herbivore whose condition is not dominated by the influence of hunting, and a forest protected from commercial logging —the beauty of which is also witnessed by thousands of human visitors each year. Those natural processes would seem to be a crown jewel for the National Park Service that can be readily preserved for the foreseeable future.
2. For example, primary evidence for thinking that Isle Royale moose are exotic is an unidentified elderly man saying, in the parking lot of a gas station in Manitoba in the early 1950s, that humans brought moose to Isle Royale. Secondary evidence is that Tim Cochrane believes it is unlikely that moose would have colonized Isle Royale by swimming, given the distance and cold temperature of the water. Documented movements of moose among islands off the coast of British Columbia, Norway, Sweden, and Finland indicate that moose are more than capable of such movements. There are also eyewitness accounts of moose swimming long distances in the waters between Isle Royale and Canada. In addition, the colonization of any terrestrial mammal to an island would seem to be an unlikely event—yet it happens. Colonization, like so many natural phenomena, is undeniably remarkable, but not untenable. If humans had brought moose to Isle Royale in the early 20th century it would have been a newsworthy event. One of us (ROP) reviewed newspapers from the north shore of Minnesota (Two Harbors, MN) in the early 20th century and found no reporting of such an event.
3. Cochrane (2013) indicates that implementing a moose harvest should be considered as a means of replacing the effect of wolf predation. In a typical year, wolves kill about 100 Isle Royale moose. To implement a moose harvest of that intensity in a place as remote as Isle Royale during the spring, fall, or winter when the weather is frequently prohibitive seems untenable. There is also reason to be concerned with the outrage that many citizens would likely express against such a plan.
4. For example, a photo from the 1930s of Otto Olson with the pelts of canids that he

trapped on Isle Royale includes a specimen that could, on the basis of its size, easily be a wolf.

5. The plausibility of various elements of wolves' history on Isle Royale, as conveyed in Cochrane (2013), depends on a biological understanding of wolves in general and on Isle Royale in particular with which we do not agree. Space limitation precludes elaboration.
6. This result assumes the relationship between kill rate and growth rate is best described by a logarithmic relationship; see Vucetich and Peterson (2004).
7. Since the early 1960s, the incidence of malformation has increased to the point that every collected specimen born after 1995 has exhibited some kind of vertebral malformity.
8. To say that considerable evidence exists for believing that inbreeding depression places Isle Royale wolves at great risk of extinction is not to say that we alone are impressed by the weight of evidence. We have also solicited the views of others with expertise in conservation genetics, including L. Boitani, University of Rome; R. Frederickson, University of Montana; P. Hedrick, Arizona State University; R. Lacy, Chicago Zoological Society; O. Liberg, *Swedish* University of Agricultural Sciences; L. Waits, University of Idaho; R. Wayne, University of California–Los Angeles. It also appears to be the collective judgment of experts in conservation genetics who are familiar with the Isle Royale case that inbreeding depression places the park's wolves at considerable risk of extinction. In scientific discourse, when two sets of scholars (e.g., Mech [2013] and us) disagree about the significance or interpretation of scientific evidence, the solicitation of expert opinion in a robust manner from a number of experts is an important basis for better understanding (Sutherland 2006; Martin et al. 2012).
9. Again, the view expressed in this paragraph appears to be the collective judgment of experts in conservation genetics who are familiar with the Isle Royale case. One technical concern with expecting to learn anything significant by observing the time to extinction for the Isle Royale population is that the inherent variability of times to extinction, as a statistical phenomena, is notorious. That inherent variability severely limits what can be learned about extinction risk and the factors that influence extinction risk by observing the time to extinction of a single population (Foley 1994; see also Vucetich and Waite 1999).
10. Some natural resource managers assert, as we understand it, that significant scientific knowledge would result from observing the effect of moose on Isle Royale in the absence of wolf predation. Yet the degradation of ecosystem health in the absence of top predators is thoroughly studied. National parks, in particular, have contributed greatly to knowledge of that subject (e.g., Yellowstone, Rocky Mountain, and Great Smoky Mountains national parks). Moreover, in the mid-20th century, awareness of the damage caused by moose in the absence of wolf predation on Isle Royale led conservation leaders, including Aldo Leopold, Adolph Murie, and Sigurd Olson, to conclude that wolves should have been introduced to the national park at that time.
11. We clearly indicated as such in Peterson et al. (1998).
12. Throughout the 1980s and early 1990s, Isle Royale wolf abundance was low—likely due to the combined influence of disease and inbreeding depression. The species' rebound was almost certainly attributable, at least in part, to the genetic rescue that occurred

when an immigrant wolf arrived on Isle Royale in 1997.

13. Mech (2013) also explains that the climate is expected to become increasing variable and that variability might increase the frequency of particularly cold winters that would produce ice bridges upon which wolves might use in immigrating to Isle Royale. That expression of optimistic possibility is at odds with what is likely to occur. In particular, while climate is expected to become more variable, that variability is expected to be associated with an increased frequency of warm winters and a decreased frequency of cold winters (e.g., Meehl et al. 2009) and reduced ice cover on Lake Superior (Wang et al. 2012).
14. The abundance of beaver colonies on Isle Royale also increased by approximately 60% with the collapse in predation that began in 2012. A prolonged period of elevated beaver abundance would also very likely have considerable and long-lasting impacts on forest dynamics.

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