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Sustainability of Natural Populations: Lessons from Indigenous Knowledge

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Sustainability of Natural Populations: Lessons from Indigenous Knowledge

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Management schemes for wildlife are often unsuccessful in maintaining healthy, sustainable populations, especially approaches based on Maximum Sustainable Yield, which fail to account for variation in reproductive output. North American Indigenous hunters had considerable knowledge about the dynamics of local populations and were aware that they were subject to major fluctuations. These peoples developed the concept of "Keepers of the Game," which suggested that if fish or game animals were not treated with proper respect, these "keepers" could remove their population, making it unavailable for human exploitation. The "keepers" concept may have represented recognition of exceptional individuals that had unusual influence on local population dynamics. Existence of such individuals has been established empirically through long-term studies that show that less than 10% of a cohort may contribute 75–90% of recruits to succeeding generations. Incorporation of this concept into management schemes might lead to increased sustainability of wildlife populations.

Keywords Indigenous peoples, hunting, population biology, wildlife, reproductive output

A major focus of research in resource management and conservation biology is the development of management schemes for the harvest of populations of fish, mammals, birds, and exploitable plants that maintain sufficiently high populations so that they can be harvested well into the future (Ashley, 2003; Coltman, 2003; Conover & Munch, 2002; Palumbi, 2001; Turner, 2005). These models, however, have not been successful in many cases because managed populations have been driven close to commercial extinction as a result of the very practices that have been employed in an effort to achieve sustainability (Milner-Gulland, 2003; Myers & Worm, 2003, 2005). A common conceptual framework that appears to contribute to these collapses is the assumption of a "balance" within nature. The goal of this study is to examine the assumption of the "balance of nature" from a different sociocultural perspective, and suggest an alternative pathway to sustainability of exploited populations.

A clear alternative emerges from the tradition of the Indigenous peoples of North America, who understand populations as collections of individuals, some of which can be readily taken by hunters or fishermen, while others should not be taken or even pursued (Pierotti & Wildcat, 2000). Such traditions teach that productivity in animal populations is regulated by specific individuals, referred to as "animal bosses," "keepers of the game"

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(C. Martin, 1978), "animal masters" (Harrod, 2000; Tanner, 1979), or those "who cannot be killed" (Brown, 1992).

The potential usefulness of these Indigenous ideas can be discussed in the context of data from Western scientific studies, conducted in the last twenty-five years. These long-term studies of natural populations reveal unexpectedly high variability in individual lifetime reproductive performance (Clutton-Brock, 1988; Newton, 1989) that is not accounted for within the theoretical framework used by resource managers and may be a clue to the problems inherent in sustainable harvest models.

The History of Models for Managing Wild Populations

Within the "balance of nature" framework, ecosystems, ecological communities, and animal populations are presumed to exist most of the time under equilibrium conditions to which they are inclined to return any time they experience a perturbation. The roots of this framework lie in Western scientific philosophy dating back to Bacon and Linnaeus (Worster, 1994: Chapter 2). A key statement that illustrates the use of this concept can be found in Darwin (1859) ". . . the forces are so nicely balanced that the face of nature remains uniform, for some time . . ." This concept continues into contemporary science as can be seen in statements by well-respected European investigators (e.g., "There is a balance, there is an almost permanence about such animal communities. We see the stability, the lack of change") (Kruuk, 2002, p. 55).

Such ideas were given mathematical form by the Lotka-Volterra equations developed in the 1920s (Kingsland, 1985). As a consequence, researchers often assumed that "balance" was an actual state that ecosystems strove to attain. Associated with the metaphor of balance were the assumption of the literal truth of "equilibrium" communities and the existence of "*K*-selected populations." A *K*-selected population is assumed to reach a carrying capacity at which population numbers remain relatively constant and population size is maintained almost exclusively through density dependent processes resulting from intraspecific competition (Lack, 1954; MacArthur, 1972; see also Kingsland, 1985, 2005).

The twinned metaphors of balanced ecosystems and equilibrium populations led to a widespread but unsuccessful model for the exploitation of natural populations of birds, fish, and mammals, that proposes that populations can exist at a level that allows them to be harvested at a "Maximum Sustainable Yield" (MSY) and that all individuals within the population are potentially subject to harvest (Holt, 1975; Ricker, 1975; Larkin, 1977). The MSY concept has been described as "based on a myth that nature is stable" and that "assumes inherent stability and constant productivity" (Wilson, 2005). Under this model it is assumed that it is possible to exploit a population maximally when it is near one half of its carrying capacity (Ricker, 1975; Larkin, 1977; Mangel, Marinovic, Pomeroy, & Croll, 2002). MSY models thus employ a major "simplifying assumption" that emerges from the idea of a "carrying capacity" that population sizes of fish and wildlife are regulated almost exclusively by competition within a species. Environmental fluctuations are presumed to be of little consequence (Holt, 1975; Ricker, 1975; Larkin, 1977; Wilson, 2005); however, under fluctuating environmental conditions, carrying capacities (*K)* are hard to define and probably do not exist in any meaningful sense (Pierotti, 1991) thereby invalidating the basic assumptions of the MSY model.

In Western society, social, economic, and political pressures often result in management decisions that allow fishermen to continue to heavily exploit populations, even when they seem to be in decline. This is because shutting down fisheries, as was done with the Cod fishery on the Grand Banks, leads to unemployment and even collapse of local economies.

The failure to understand details of local population dynamics, combined with political and economic pressure which emphasize taking the largest individuals available, has led to disastrous crashes of large numbers of fish populations throughout the world (Kurlansky, 1997; Myers & Worm, 2003, 2005; Wilkinson, 2006). Despite repeated failures, MSY remains government policy of many countries and states, including the National Marine Fisheries Service of the National Oceanic and Atmospheric Administration (NOAA) (Worm, 2009).

An often unstated simplifying assumption underlying MSY and other equilibrium-based models is that all individuals in a population are equivalent and can be substituted for one another (Holt, 1975; Larkin, 1977). A related assumption is that if a dominant animal is harvested, it can be readily replaced by another member of the population. Thus, Western science tends to largely ignore variation among adults in a given population or social system. As an example, Nobel prize–winning ethologist Niko Tinbergen's classic study on the behavior and ecology of gulls *The Herring Gull's World* (1953) is built on the assumption that describing the breeding behavior and ecology of an archetypical Herring Gull is sufficient to describe these phenomena for all members of the species (Burghardt, 1997). This state of affairs has become even more solidified with contemporary systematics, where highly variable behavioral characters, such as parental care, mating system, or foraging mode are considered to be species-typical traits that can be employed as character states in phylogenetic analysis (Brooks & McLennan, 1991).

Some Western scientists have suggested more realistic models (e.g., Mertz, 1971a,b), but these alternatives were pushed aside in the quest for balance-based, equilibrium explanations, such as the mania for "*r* and *K* selection" that swept population and evolutionary ecology in the 1970s (Boyce, 1984; MacArthur, 1972; Pianka, 1970). The MSY concept has been described as "based on a myth that nature is stable" and that "assumes inherent stability and constant productivity" (Wilson, 2005). "MSY . . . seems to have a life of its own . . . still being influenced by Huxley's teaching about the resilience of indestructible nature. The idea seems to have more resilience than nature itself . . . the theory cannot be killed by mere experience" (Kurlansky, 1997; Mangel et al., 2002).

Indigenous Perspectives

Alternative approaches are needed that are not simply variations on MSY. In the traditional beliefs of many Indigenous peoples of North America "animal, fish, and plant species functioned as societies . . . and each local band of a particular species was said to have its own boss . . . these beings were very real to them (Indigenous people). . . . To see one of them was a rare privilege indeed" (Martin, 1978, p. 71). The term "boss" seems to have been a recent development; traditionally such individuals were described as "masters" or "keepers" of the game (Martin, 1978). "Keepers of the Game" (my term of choice) are characterized as entities that determine whether or not their species will continue to be available for exploitation by humans. The underlying tradition is that if humans are greedy and hunt to excess, the Keepers will withdraw their species from being accessible to humans (Barsh, 2000; Harrod, 2000; Martin 1978; Nelson, 1983; Tanner, 1979).

"Keepers of the Game" have often been considered by Western anthropologists to be spirits, or to be mythological constructs that serve a symbolic purpose somewhat akin to Platonic "ideals" (Martin, 1978; Pierotti, in press). Nelson (1983) specifically refers to *biyeega hoolaanh* of the Koyukon people as, "powerful spirits who can harm anyone who offends them, taking away luck in hunting and trapping" (p. 22). Traditions of "keepers" are widespread and found among numerous tribal nations in almost all bioregions across

Table 1
Indigenous American Nations that have been recorded as having a concept similar to Keepers of the Game as defined in this article

Tribal nation	Term used (translated into English)	Source(s)
Northern Plains: Cheyenne	Animal Master	Harrod (2000)
Lakota	Those who cannot be killed	Brown (1992)
Southern Woodlands: Cherokee	Deer Chief	Awiakta (1993), Martin (2000)
Northern Forests: Ojibwe	Keeper of the Game	Martin (1978)
Northeast: MicMac	Animal Bosses	Martin (1978)
Seneca	Old Man Beaver	Dennis (1986)
Northern Boreal Forest: Mistassini Cree	Animal Master	Tanner (1979)
Naskapi	Caribou Man	Speck (1935)
Innu	Animal Spirits	Henriksen (2009)
Northwest and Alaska: Kluane	Animal Teachers	Nadasdy (2003)
Koyukon (Athabascan)	biyeega hoolaanh	Nelson (1983)

North America (Table 1), which suggests this is a widely held concept. Martin (1978) states that "keepers" were very real to Indigenous people. Indigenous "legends" or stories about animals should be considered as metaphors that serve the same function that theoretical models serve in ecology (Pierotti, in press)—they present a generalized and oversimplified picture, based on a number of simplifying assumptions, some of which are based in knowledge and others are logical consequences of the structure of the model. Both models and stories are metaphoric structures, which serve a heuristic purpose by imparting insights into how complex processes actually function (Pierotti, in press).

I argue that stories of "keepers" are based upon actual experience with extraordinarily successful or experienced individual animals—if individual animals that would have contributed a preponderance of recruits to succeeding cohorts are killed, or even harassed to such an extent that they are driven away, then a local population that depended on their output could go "functionally extinct," which is equivalent to making their kind unavailable to humans, or of taking away "luck in hunting or trapping.

Empirical Evidence Supporting "Keepers of the Game"

All non-human animals are individuals that function within both a social (population) and historical (evolutionary) context. In the 1970s scientists began to study individually recognizable animals in an effort to understand the evolution of behavior and social systems. The results of such studies were then used to examine individual variation in lifetime reproductive success (LRS) (Clutton-Brock, 1988; Newton, 1989). The results of 25 individual long-term studies that provided data on LRS in birds and mammals all showed the same pattern (i.e., that about 10% of a breeding population can generate up to 85% of the recruits to succeeding generations) (Table 2; Annett & Pierotti, 1999; Newton, 1989).

To show evidence for the literal existence of "keepers," data collected from two long-term studies of lifetime breeding output in free-living populations will be used. These

Table 2
Species that show dramatic skews in individual lifetime reproductive output

Birds	Mammals
Great Tit, *Parus major* (Netherlands)[1]	Red Deer, *Cervus elaphus*[1]
Great Tit, *Parus major* (Netherlands)[1]	African Lion, *Panthera leo*[1]
Great Tit, *Parus major* (England)[1,2]	Northern Elephant Seal, *Mirounga angustirostris*[1]
Blue Tit, *Parus caeruleus*[2]	
Song Sparrow, *Melospiza melodia*[1,2]	
Meadow Pipit, *Anthus pratensis*[2]	
Splendid Fairy Wren, *Malurus splendens*[2]	
Indigo Bunting, *Passerina cyanea*[2]	
Red-winged Blackbird, *Agelaius phoeniceus*[2]	
Florida Scrub Jay, *Aphelocoma coerulescens*[1,2]	
House Martin, *Delichon urbica*[1,2]	
Green Woodhoopoe, *Phoeniculus purpureus*[2]	
Sparrowhawk, *Acciptier nisus*[1,2]	
Osprey, *Pandion haliaetus*[2]	
Ural Owl, *Strix uralensis*[2]	
Bewick's Swan, *Cynus columbianus*[1]	
Mute Swan, *Cygnus olor*[2]	
Barnacle Goose, *Branta leucopsis*[2]	
Black-legged Kittiwake, *Rissa tridactyla*[1]	
Red-billed Gull, *Larus novaehollandiae*[2]	
Western Gull, *Larus occidentalis*[3]	
Northern Fulmar, *Fulmarus glacialis* 1	
Black Grouse *Tetrao tetris*	

Data from [1]Clutton-Brock (1988), [2]Newton (1989), [3]Annett and Pierotti (1999).

studies provide an understanding of the ecology and underlying social dynamics. Both studies were conducted on large, long-lived, low fecundity species that would be presumed to show K selected life history tactics as described by Pianka (1970, 2000). According to classical models of equilibrium populations there should be little variability in adult reproductive performance in populations of such species.

One long-term study of Northern elephant seals, *Mirounga angustirostris*, during breeding seasons of 1971 and 1972 was conducted on Ano Nuevo Island, San Mateo County, California. All animals in this population were tagged in the webbing of their hind flippers using cattle ear tags with unique numbers. Adult males, along with some adult females, were also marked by using Lady Clairol Ultrablue hair dye to bleach a three or four letter code on their sides that allowed them to be identified more easily from a distance. The performance of each individual was assessed by noting the number of successful copulations for each male and the number of years that a female gave birth to a living pup (LeBoeuf, 1974; LeBoeuf & Reiter, 1988). More than 90% of mammalian species show a polygynous mating system (Lack, 1968; Pierotti, 1981); in such species it is expected that there might be considerable variation among males in reproduction, but not amongst females.

The second study was a 13-year-long (1983–1995) study of a population of Western Gulls, *Larus occidentalis*, on Alcatraz Island, San Francisco County, California in which birds were individually banded using U.S. Fish and Wildlife Service metal bands with unique numbers. Gulls were monitored during nest checks that took place 2–3 times a week, supplemented by observation from a plywood blind. This routine allowed assessment of number of eggs laid, number of chicks hatched, and the survival of chicks to fledging (Annett & Pierotti, 1999). Chicks were banded at approximately one week of age using F&WS bands. Western Gulls are large-bodied, long-lived, and monogamous (90% of bird species are considered to be monogamous; Lack, 1968), which represents the sort of life history shown by species often exploited as game birds, or used for food by human subsistence hunters.

Northern Elephant Seal Case Study

The initial results suggested that there might be an empirical basis to the idea of "Keepers of the Game," This population of Northern elephant seals had one male (marked as ADR), who, even as he was aging, appeared to use a distinct set of tactics to become the most successful male breeder in his local population for three consecutive years. He conserved energy, while allowing other males to fight for position and status, and only challenging the winners near the peak of female receptivity. This revealed that free-living populations contained individuals who appeared to be much better than others at behavioral tactics that allowed them to maximize reproductive output.

Subsequent population analysis showed high variation in lifetime reproductive output for both male and female elephant seals (LeBoeuf & Reiter, 1988). Most of the male offspring (of 151 male pups tagged as newborns) during 1964–1967 (87%) did not even survive to reproductive age (Figure 1). Of the 19 males that did survive to reproductive age, an additional 11 (7%) died without being observed to copulate (Figure 1). Thus almost 95% of male elephant seals in two distinct cohorts failed to breed during their lifetimes. Of the eight males (5%) that fathered offspring, only three (2% of the cohort) produced more than 20 offspring (Figure 1). These three individuals fathered 281 (81%)

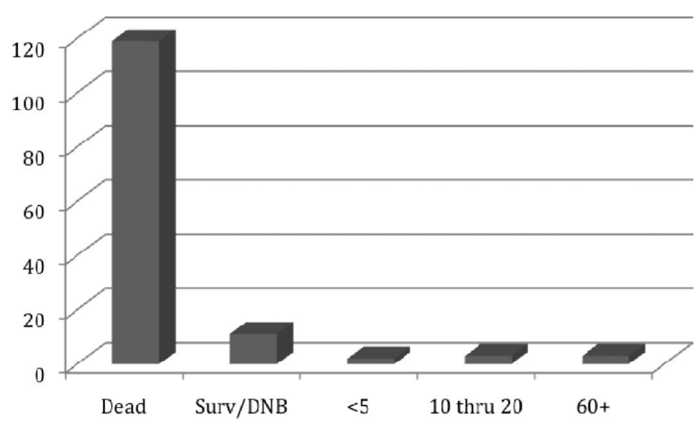

Figure 1. Distribution of lifetime reproductive success (LRS) in male Northern Elephant Seals, *Mirounga angustirostris* on Ano Nuevo Island, California from LeBoeuf and Reiter (1988). Y axis is number of individual adults, X axis is LRS as indicated by number of pups fathered (Dead = died before reaching reproductive age; Surv/DNB = survived to reproductive age but failed to reproduce).

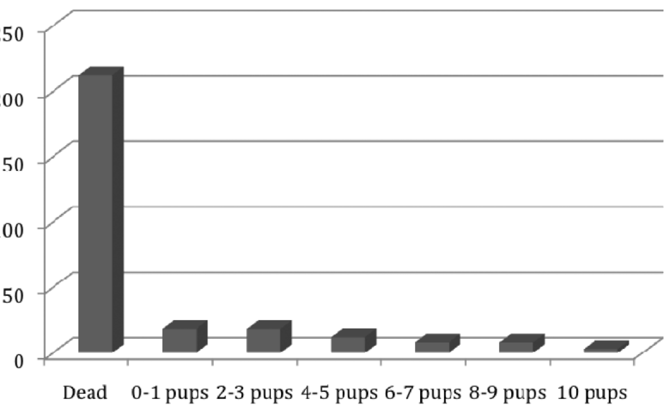

Figure 2. Distribution of lifetime reproductive success (LRS) in female Northern Elephant Seals, *Mirounga angustirostris* on Ano Nuevo Island, California from LeBoeuf and Reiter (1988). Y axis is number of individual adults, X axis is LRS as indicated by number of pups produced that survived to weaning (Dead = died before reaching reproductive age).

out of 348 total offspring. Individual outputs of these males were 121, 97, and 63 offspring. I suspect that ADR exceeded any of these individual totals during his three-year term as most successful male (ADR was born prior to the initiation of the study, therefore his exact age was unknown).

Elephant seals are highly polygynous, so there is a significant difference in potential male and female lifetime performance (LeBoeuf, 1974). Overall variance was lower for female Northern elephant seals, but still turned out to be much higher than expected (see Figure 2). Of 279 females that survived to weaning out of 344 female pups born in 1973 (n = 102) and 1974 (n = 177), only 67 (24%) survived to breeding age (2–5 years; LeBoeuf & Reiter, 1988). Of these 67, only eight total: two from the 1973 cohort (1.9%) and six from the 1974 cohort (3.4%) survived to reproduce for at least ten years, producing a single pup each year of their lives from ages three or four through fourteen (Figure 1; see LeBoeuf & Reiter, 1988 for further details).

The clear result from this study was that even in a polygynous mammal, very few individuals (three males and eight females out of over 400 individuals in these combined cohorts) made disproportionately high contributions to future populations of a large marine mammal. High variance might be expected in males, where only 5% produced all the offspring, and 2% fathered more than 80% of the next generation. More surprising was that 78% of female elephant seals had no breeding success, and only 3% of these females were highly successful (i.e., producing ten or more offspring) (LeBoeuf & Reiter, 1988). Thus, even in a species that produces only a single offspring/reproductive event, a small percentage carried the population, making significant contributions to its persistence. More interesting, the most successful female seals began breeding at the age of two or three years, which is below the population mean, which suggests that they are effectively immune for costs of reproduction, which assume a trade-off between survival and fecundity (Bell, 1980; Roff, 1992; Stearns, 1976, 1992).

Elephant seals do not hold breeding territories, so if any of these few highly successful individuals had been killed, their contribution to future generations would have been lost and subsequent local population sizes would have been much smaller or might even have disappeared altogether. From the perspective of a harvester, almost any individual seal could have been killed for food, provided that they did not kill the few highly successful individuals.

Western Gull Case Study

Early work on gulls (*Larus*) emphasized how individual males and females adjusted nesting and foraging behavior in response to local environmental conditions, to the time and energy budget requirements of their mates, and to the process of reproduction (Pierotti, 1981, 1982, 1987; Pierotti & Annett, 1990, 1991). Western scientific traditions largely ignore variation among parents, the quality of the care they provide, and the effects of such variation on breeding success, instead assuming that parental care is a species-specific trait and that individual variation was unimportant.

During our 13-year study of individual variation in lifetime breeding success in Western Gulls on Alcatraz (Annett & Pierotti, 1999), we did not assess survival to reproduction as was done in the elephant seal work, but simply looked at the lifetime breeding performances for pairs of adults (age 4+ for males, 5+ for females; Pierotti and Annett, 1995). We found (a) a high level of variation in individual lifetime reproduction (0–30 offspring produced), (b) most individuals were relatively unsuccessful (modal production of offspring among breeders was 0), and (c) only about 6% (nine of 130 pairs) were highly successful (20+ fledged offspring), and made a substantial contribution to future recruitment (Figure 3). Western Gulls do hold breeding territories, but these are not used for feeding and ample breeding space was available, so there was no limiting resource that these pairs could control. Territories held by highly successful pairs did not differ in obvious ways from those held by less successful pairs. If any of these pairs, or even one member of the pair, had been killed, the population would not have grown well. In fact, we did lose one female from a pair that showed potential of being highly successful (four straight years of producing three healthy fledglings each year). As a consequence of her death, that portion of the colony had only a few unsuccessful breeders for the remainder of the study and declined in number, which shows the possible consequence of losing an exceptional

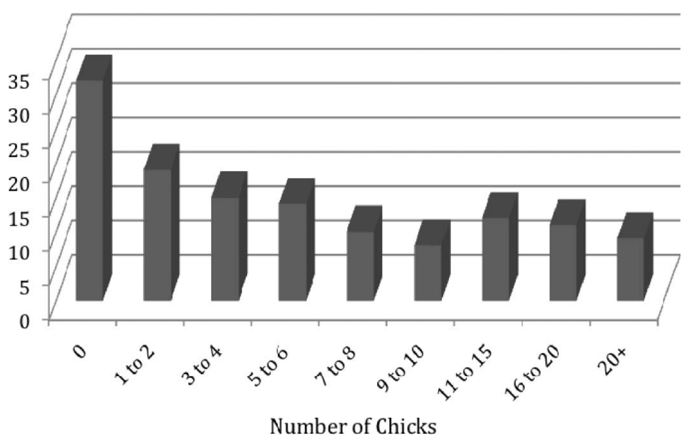

Figure 3. Distribution of lifetime reproductive success in pairs of Western Gulls, *Larus occidentalis* on Alcatraz Island, San Francisco, California from Annett and Pierotti (1999). Y axis is number of individual pairs (one male and one female), X axis is LRS as indicated by number of offspring that survived to fledging (independence from parents).

individual. To emphasize the point made above about limiting resources, her nesting territory was not taken over by another pair after her passing.

Discussion and Conclusions

The logic that appears to underlie the Indigenous concept of “Keepers of the Game” is that if individuals that contribute the bulk of successful reproduction for an important species were driven off by human activities, this could lead to serious declines, even possible local extinctions. North American Indigenous peoples pay close attention to the natural world and look carefully at individuals (Pierotti, in press). Thus, they were fully aware of the existence of such beings and probably integrated information about such entities into their combined knowledge and spiritual systems (Barsh, 2000; Pierotti and Wildcat, 2000). For example, the Kluane First Nation of Canada opposed sport hunting of Dall Sheep because they argued that older more experienced (full curl) males are especially important to the overall sheep population because of their role as “teachers.” Younger rams learn proper mating and rutting behavior as well as more general survival strategies from these older more experienced males (Nadasdy, 2003). Western scientists have made similar arguments (Coltman, 2003), but in this latter case, they employ a mechanistic argument, assuming that trophy males are genetically superior, rather than stressing social reasons.

Western science has traditionally failed to recognize the importance of traditions and social structures in non-humans (de Waal, 2000; Laland & Galef, 2009). Despite extensive evidence of cultural traditions in non-humans, there remains a debate in Western science over the very existence of culture in non-humans. Investigators who argue for existence of culture, or even cognition, in non-humans are accused of anthropomorphism (Budiansky, 1998; Kennedy, 1992). To North American Indigenous peoples, the existence of cultural traditions in non-humans is a natural component of traditional knowledge. It is assumed that animals have the ability of cognition (Anderson, 1996), and that information is passed on to others across generations about locations of good feeding areas, the most effective ways to hunt (e.g., Henriksen, 2009).

Respecting such experienced individuals would have been an effective way of minimizing the chance of local population crashes, whereas taking such individuals would mean loss not only of their reproductive output, but also the knowledge they could hold. In sperm whales, *Physeter catodon*, it has been argued that killing larger, more experienced females has led to local population extinctions (Whitehead, 1998a, b). In a similar vein, in African elephants, *Loxodonta africana*, removal of matriarchs leads to local group extinctions (Payne, 2000).

Whenever the oldest, most experienced members of an animal social group are killed or driven off, this is likely to lead to reduced abundance, and thus to possible starvation in people who depended on these populations for subsistence. The consequences predicted by Indigenous peoples have come true, with the collapse of fisheries worldwide (Kurlansky, 1997; Clover, 2008), and declines in whale and other marine mammal populations (Holt, 1975; Estes, 1979). Experience of similar events would almost certainly have generated stories and traditions among Indigenous peoples in which highly successful individuals were given special status.

A possible example of such restraint on the part of North American Indigenous peoples can be observed in results from hunting of deer prior to the arrival of Europeans (Kay, 2002). When the age structure of white-tailed deer taken by wolves (Figure 4a) is compared to the age structure of mule deer found in a thousand-year-old midden used by Indigenous Americans in Colorado (Figure 4b), it is clear that deer taken by wolves

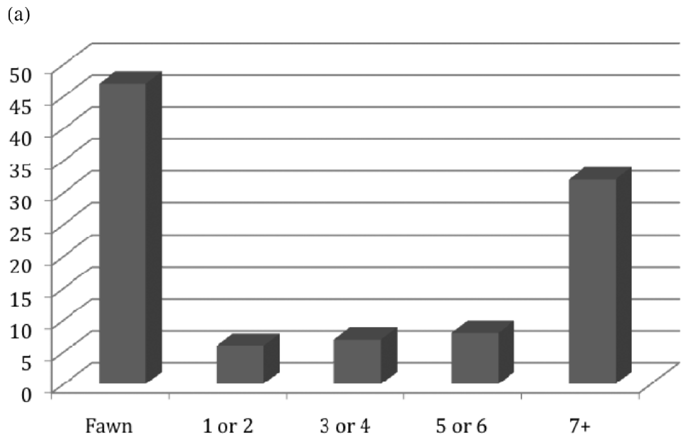

Figure 4a. Age distribution of white-tailed deer (*Odocoileus virginianus*) taken as prey by wolves in Minnesota, from Kay (2002).

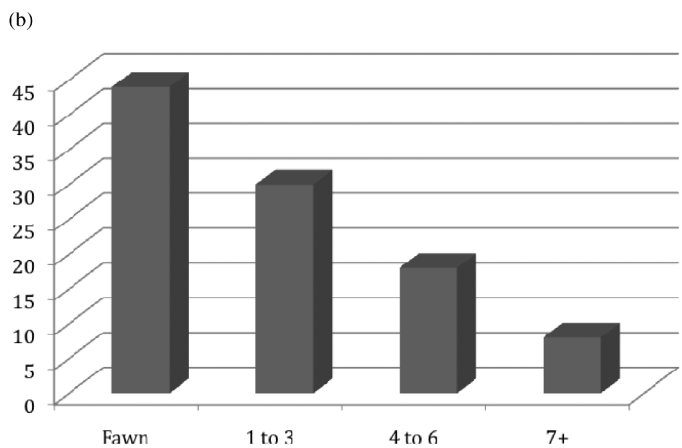

Figure 4b. Age distribution of mule deer (*Odocolieus hemionus*) taken by Indigenous American hunters prior to arrival of Europeans in North America, from Kay (2002).

include a high proportion (around 30%) of older animals, whereas older animals represent the age group taken least by Indigenous human hunters. Kay argues that these data show that human hunters took many more prime-age (1–6-year-old) individuals, whereas these age classes are hard for wolves to take. Another interpretation is possible given the results discussed in this article, that is, that human hunters deliberately avoided taking the oldest and most experienced individuals, because they considered these to be the "keepers" of the local deer population.

Europeans, who remained unaware that such variation existed among animals until the 1980s, would probably consider stories that discussed such beings to be legends concocted by "ignorant savages." In reality, however, stories about Keepers of the Game may be a more realistic description of actual population dynamics than many Western heuristic tools that have been applied to game populations, despite regular findings that they are not effective for managing populations of large long-lived, low fecundity species, such as marine mammals (Estes, 1979; Holt, 1975).

Western sport hunting (commercial hunting has been largely banned in recent decades; a situation that has recently also become the case for inland fisheries because of low population levels) focuses on "trophy" animals, typically the largest and healthiest members of their populations (Coltman, 2003; Harris, Wall, & Allendorf, 2002), and potentially those who would make the largest contribution to future generations. Thus, Western management activities concentrate on removing the very individuals that Indigenous knowledge suggests should be carefully avoided when hunting or fishing. Fishing focused on taking the largest individuals has led to stunting and, the loss of most fecund members of their kind (Kurlansky, 1997; Myers & Worm, 2003, 2005; Wilkinson, 2006). Subsequent evolutionary responses have led to reduced age and size at first reproduction in whales (Gaskin, 1982; Holt, 1975), elephant seals (*Mirounga leonina*; Laws, 1956). Hunting pressure on large "trophy" males has led to declines in both body and horn size in bighorn sheep (*Ovis canadensis*; Coltman, 2003) and to the collapse of the breeding system in saiga antelope (Milner-Gulland, 2003).

Every investigation that has examined the functional basis of this high variation in LRS found differences in foraging behavior between successful and unsuccessful individuals. In red deer (*Cervus elaphus*) on Rhum, highly successful individuals control grazing areas where the forage is higher in quality (Clutton-Brock, 1988). In Galapagos finches, individuals with the greatest success held areas where high quality food was more abundant (Grant & Grant, 1989a,b, 1995). In our gull study, successful birds fed predominantly on fish, whereas less successful individuals fed predominantly on human refuse (Annett & Pierotti, 1999). This is almost certainly culturally transmitted, because male offspring, who stay with their parents after fledging, acquired parental diets, whereas female offspring, who disperse after fledging, did not (Annett & Pierotti, 1999). Not only do a few individuals within a population show unusually long lifespans combined with high rates of reproduction, but such individuals are also likely to be repositories of knowledge that can be passed on to their descendants.

Looking at evolution, ecology, and population biology from an Indigenous perspective could generate new perspectives to solve problems that have not yielded to Western materialist metaphors. Some recent approaches taken by Western scientists have yielded perspectives that are convergent on Indigenous traditional views (e.g., recognition of cultural traditions in non-humans). Western science has long assumed that there exists a single identifiable "truth," and that it has a monopoly on appropriate approaches to discovering such "truth"; however, the widespread failure of MSY models in fisheries and wildlife management indicates that additional "truths" may be needed if we are to develop sustainable population management schemes.

Indigenous people have considerable empirically derived knowledge about the natural world, combined with a philosophical approach different from that found in any Western philosophical tradition (Suzuki & Knudtson, 1992; Pierotti & Wildcat, 2000; Pierotti in press). Following traditions derived from Indigenous philosophy could allow humans to connect to the natural world at an experiential and spiritual level that provides much more meaningful connection than is often generated by the rather abstract and allegedly objective approaches of Western science. The results I report suggest that Western science should integrate Indigenous concepts and pay more attention to individual variation within the context of long-term population studies if we expect to have sustainable populations of both commercial and game fish and wildlife for the foreseeable future. An added value of such an approach is that it would require us to rethink the underlying values of our relationship with "exploited populations" and build a more respectful relationship with the natural world.

References

Anderson, E. N. (1996). *Ecologies of the heart: Emotion, belief, and the environment*. New York: Oxford University Press.

Annett, C. A., & Pierotti R. (1999). Longterm reproductive output and recruitment in western gulls: Consequences of alternate foraging tactics. *Ecology, 80,* 288–297.

Ashley, M. V. (2003). Evolutionarily enlightened management. *Biological Conservation, 111*, 115–123.

Awiakta, M. (1993). *Selu: Seeking the Corn Mother's wisdom*. Golden, CO: Fulcrum Press.

Barsh, R. L. (2000). Taking Indigenous science seriously. In S. A. Bocking (Ed.), *Biodiversity in Canada: Ecology, ideas, and action* (pp. 152–173). Toronto, ON: Broadview.

Bell, G. (1980). Costs of reproduction. *American Naturalist, 116*, 45–76.

Boyce, M. S. (1984). Restitution of r- and K-selection as a model of density-dependent natural selection. *Annual Review of Ecology and Systematics, 15*, 427–447.

Brooks, D. R., & McLennan, D. A. (1991) *Phylogeny, ecology and behavior: A research program in comparative biology*. Chicago: University of Chicago Press.

Brown, J. E. (1992). *Animals of the soul: Sacred animals of the Oglala Sioux*. Rockport, MA: Element Press.

Budiansky, S. (1998). *If a lion could talk*. New York: Free Press.

Burghardt, G. M. (1997). Amending Tinbergen: A fifth aim for ethology. In R. W. Mitchell, N. S. Thompson, & H. L. Miles (Eds.), *Anthropomorphism, anecdotes, and animals* (pp. 254–276). Albany, NY: SUNY Press.

Clover, C. (2008). *The end of the line: How overfishing is changing the world and what we eat*. Berkeley: University of California Press.

Coltman, D. W. (2003). Undesirable evolutionary consequences of trophy hunting. *Nature, 426*, 655–658.

Conover, D. O. & Munch, S. B. (2002). Sustaining Fisheries yields over evolutionary time scales. *Science*, *297*, 94–96.

Clutton-Brock, T. H., ed. (1988). *Reproductive success: Studies of individual variation in contrasting breeding systems*. Chicago: University of Chicago Press.

deWall, F. B. (2001). *The ape and the sushi master*. New York: Basic Books.

Darwin, C. (1859). *The origin of species by means of natural selection*. London: Studio Editions.

Dennis, M. J. (1986). *Cultivating a landscape of peace: The Iroquois New World*. Ph.D. Dissertation, University of California at Berkeley.

Estes, J. R. (1979). Exploitation of marine mammals: r selection of K strategists. *Journal of Fisheries Research Board of Canada, 36*, 1009–1017.

Gaskin, D. E. (1982). The *ecology of whales and dolphins*. London: Heineman.

Grant, B. R., & Grant, P. (1989a). Natural selection in a population of Darwin's finches. *American Naturalist, 133*, 377.

Grant, B. R., & Grant, P. (1989b). *Evolutionary dynamics of a natural population: The large cactus finch of the Galapagos*. Chicago: University of Chicago Press.

Grant, B.R., & Grant, P. (1995). Predicting microevolutionary responses to directional selection on heritable variation. *Evolution, 49*, 241–251.

Harris, R. B., Wall W. A., & Allendorf, F. W. (2002). Genetic consequences of hunting: What do we know and what should we do? *Journal of Wildlife Management, 55*, 243–249.

Harrod, H. I. (2000). *The animals came dancing: Native American sacred ecology and animal kinship*. Tucson: University of Arizona Press.

Henriksen, G. (2009). *I dreamed the animals: Kaniuekutat, the life of an Innu hunter*. New York: Berghahn Books.

Holt, S. J. (1975). The concept of Maximum Sustainable Yield (MSY) and its application to whaling. *FAO/UN Scientific Consultation on Marine Mammals*. Document ACMRR/MM/SC/4.

Kay, C. E. (2002). Are ecosystems structured from the top down or bottom up? A new look at an old debate. In C. E. Kay and R.T. Simmons (Eds.), *Wilderness and political ecology: Aboriginal influences and the original state of nature* (pp. 215–237). Salt Lake City: University of Utah Press.

Kennedy, J. S. (1992). *The new anthropomorphism*. New York: Cambridge University Press.

Kingsland, S. E. (1985). *Modeling nature: Episodes in the history of population ecology*. Chicago: University of Chicago Press.

Kingsland, S. E. (2005). *The evolution of American ecology, 1890–2000*. Baltimore, MD: Johns Hopkins University Press.

Kruuk, H. (2002). *Hunter and hunted: Relationships between carnivores and people*. Cambridge, UK: Cambridge University Press.

Kurlansky, M. (1997). *Cod: A biography of the fish that changed the world*. New York: Walker Press.

Lack, D. (1954). *The natural regulation of animal numbers*. New York: Oxford University Press.

Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Chapman and Hall.

Laland K. N., & Galef, B. G. (2009). *The question of animal culture*. Cambridge, MA: Harvard University Press.

Larkin, P. A. (1977). An epitaph for the concept of MSY. *Transactions of the American Fisheries Society, 106*, 1–11.

Laws, R. M. (1956). The elephant seal (*Mirounga leonina*) II. General, social and reproductive behaviour. *FIDS Sci. Report #13*. 88 pp.

LeBoeuf, B. J. (1974). Male-male competition and reproductive success in elephant seals. *American Zoologist, 14*, 163–176.

LeBoeuf, B. J., & Reiter J. (1988). Life time reproductive success in Northern elephant seals. In T. H. Clutton-Brock (Ed.), *Reproductive success: Studies of individual variation in contrasting breeding systems* (pp. 344–362). Chicago: University of Chicago Press.

MacArthur, R. H. (1972). *Geographical ecology*. New York: Harper and Row.

Mangel, M., Marinovic, B., Pomeroy, C., & Croll, D. (2002). Requiem for Ricker: Unpacking MSY. *Bulletin of Marine Science, 70*, 763–781.

Martin, C. L. (1978). *Keepers of the game: Indian-animal relationships and the fur trade*. Berkeley: University of California Press.

Martin, J. W. (2000). *The land looks after us: A history of Native American religion*. New York: Oxford University Press.

Mertz, D. B. (1971a). Life history phenomena in increasing and decreasing populations. In G. P. Patil, E. C. Pielou, & W. E. Waters (Eds.), *Statistical ecology*, vol. 2 (pp. 361–399). University Park: Pennsylvania State University Press.

Mertz, D. B. (1971b). The mathematical demography of the California condor population. *American Naturalist, 105*, 437–453.

Milner-Gulland, E. J. (2003). Reproductive collapse in saiga antelope harems. *Nature, 422*, 135.

Myers, R. A., & Worm B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature, 423*, 290–283.

Myers, R. A., & Worm, B. (2005). *Proceedings of the Royal Society of London; Series B: Biological Science, 360*, 13–20.

Nadasdy, P. (2003). *Hunter and bureaucrats: Power, knowledge, and Aboriginal/State relations in the Southwest Yukon*. Vancouver, BC: University of British Columbia Press.

Nelson, R. K. (1983). *Make prayers to the Raven: A Koyukon view of the Northern forest*. Chicago: University of Chicago Press.

Newton, I. (1989). *Lifetime reproduction in birds*. New York: Academic Press.

Palumbi, S. R. (2001). Humans as the world's greatest evolutionary force. *Science, 293*, 1786–1790.

Payne, K. (2000). *Silent thunder: In the presence of elephants*. New York: Viking Press.

Pianka, E. R. (1970). On "r" and "K" selection. *American Naturalist, 104*, 592–597.

Pianka, E. R. (2000). *Evolutionary ecology*.

Pierotti, R. (1981). Male and female parental roles in the western gull under different environmental conditions. *Auk, 98*, 532–549.

Pierotti, R. (1982). Habitat selection and its effect on reproductive output in the herring gull in Newfoundland. *Ecology, 63*, 854–868.

Pierotti, R. (1987). Behavioral consequences of habitat selection in the herring gull. *Studies in Avian Biology, 10*, 119–128.

Pierotti, R. (1991). Individual variation and the costs of reproduction. *Condor, 93,* 1039–1040.

Pierotti, R. (in press). *Indigenous knowledge, ecology and evolutionary biology*. New York: Routledge.

Pierotti, R., & Annett C. A. (1990). Diet and reproductive performance in seabirds. *Bioscience, 40*, 568–574.

Pierotti, R., & Annett C. A. (1991). Diet choice in the herring gull: Effects of constraints imposed by reproduction and ecology. *Ecology, 72*, 319–328.

Pierotti, R., & Annett C. A. (1995). Western Gull (*Larus occidentalis*). In A. Poole and F. Gill, (Eds.), *The birds of North America*. Philadelphia: The Academy of Natural Sciences, Washington D.C.: American Ornithologist's Union.

Pierotti, R., & Wildcat, D. (2000). Traditional ecological knowledge: The third alternative. *Ecological Applications, 10*, 1333–1340.

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada 191*. (Env. Fish Marine Sci., Ottawa).

Roff, D. (1992). *The evolution of life histories: Theory and analysis*. London: Chapman and Hall.

Speck, F. (1935). *Naskapi: The savage hunters of the Labrador Peninsula*. Norman: University of Oklahoma Press.

Stearns, S. C. (1976). Life history tactics: A review of the ideas. *Quarterly Review of Biology, 51*, 3–47.

Stearns, S. C. (1992). *The evolution of life histories*. New York: Oxford University Press.

Suzuki, D., & Knudtson P. (1992). *Wisdom of the elders: Sacred native stories of nature*. New York: Bantam Books.

Tanner, A. (1979). *Bringing home animals*. London: C. Hurst.

Turner, N. (2005). *The Earth's blanket: Traditional teachings for sustainable living*. Seattle: University of Washington Press.

Whitehead, H. (1998). Cultural selection and genetic diversity in matrilineal whales. *Science 282*, 1708–1711.

Whitehead, H. (2003a). Society and culture in the deep and open ocean: The sperm whale and other cetaceans. In F. B. de Waal and P. Tyack (Eds.), *Animal social complexity: Intelligence, culture and individualized societies* (pp. 444–464). Cambridge, MA: Harvard University Press.

Whitehead, H. (2003b). *Sperm whales: Social evolution in the ocean*. Chicago: University of Chicago Press.

Wilkinson, A. (2006). The lobsterman: Solving a mystery off the Maine coast. *New Yorker*, July 31, 56–65.

Wilson, K. (2005). MSY, no net loss and the future of Fraser River sockeye. Chapter 10 in *World Summit on Salmon*. Retrieved June 14, 2010, from http://www.sfu.ca/cs/science/summitWilson.htm

Worm, B. (2009). Rebuilding global fisheries. *Science*, *325*, 578–585.

Worster, D. (1994). *Nature's economy: A history of ecological ideas*. New York: Cambridge University Press.