

# Genetic effects of harvest on wild animal populations

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**Human harvest of animals in the wild occurs in terrestrial and aquatic habitats throughout the world and is often intense. Harvest has the potential to cause three types of genetic change: alteration of population subdivision, loss of genetic variation, and selective genetic changes. To sustain the productivity of harvested populations, it is crucial to incorporate genetic considerations into management. Nevertheless, it is not necessary to disentangle genetic and environmental causes of phenotypic changes to develop management plans for individual species. We recommend recognizing that some genetic change due to harvest is inevitable. Management plans should be developed by applying basic genetic principles combined with molecular genetic monitoring to minimize harmful genetic change.**

## Genetic effects of human exploitation

Humans have harvested animals from the wild since the beginning of our species. There is mounting evidence that overexploitation has led to the direct demographic extinction of many populations and species [1]. Genetic changes brought about by exploitation pose a less obvious threat than direct extinction. Nevertheless, such genetic changes might greatly increase the difficulty of managing populations so that they can be harvested sustainably [2–5].

Many resource managers have been reluctant to accept the potential for harvest to cause genetic change, and many are doubtful that any such changes are harmful [6–8]. However, intense and prolonged mortality caused by exploitation will inevitably result in genetic change. Harvest need not be selective to cause genetic change; uniformly increasing mortality independent of phenotype will select for earlier maturation [5]. Genetic changes caused by exploitation can increase extinction risks and reduce recovery rates of over-harvested populations [4,9].

## Glossary

**Allelic diversity:** a measure of genetic diversity based on the number of alleles per locus in a population.

**Candidate gene loci:** any gene thought to be associated with a disease or any phenotype likely to be affected by selection. For example, major

histocompatibility complex (MHC) loci in vertebrates are among the strongest candidate genes for disease-related studies because of extensive evidence that MHC genotypes influence disease susceptibility.

**Census population size:** the total number of individuals in a population.

**Darwinian debt:** the expectation that evolutionary recovery from harmful genetic changes caused by exploitative selection occurs over much longer timescales than those over which the changes were induced in the first place.

**Disruptive selection:** selection in which individuals at both extremes of the distribution contribute more offspring than those in the middle of the distribution.

**Effective population size ( $N_e$ ):** the size of an ideal population that would experience the same rate of genetic change through genetic drift as the observed population. There are two common measures of effective population size. The ‘variance effective number’ is based upon change in allele frequency, and the ‘inbreeding effective number’ is based upon reduction in heterozygosity.

**Exploitative selection:** selection as a result of human harvest analogous to Darwin’s use of the term ‘artificial selection’ for the intentional breeding of certain traits, or combinations of traits, over others in domestic animals and plants.

$F_{ST}$ : standardized index of the distribution of genetic variation between populations on a scale between 0 (identical allele frequencies among populations) and 1 (populations fixed for different alleles).

**Generation interval ( $G$ ):** the mean age of parents when offspring are born or hatched.

**Genetic monitoring:** quantifying temporal changes in population genetic metrics (e.g. heterozygosity of effective population size) or other population parameters (census population size) using molecular markers.

**Genetic swamping:** the loss of locally adapted alleles or genotypes caused by immigration and gene flow.

**Genomics:** the simultaneous study of numerous loci throughout the genome. Genomics is also often defined as the study of genes, their structure and function.

**Heritability ( $H_A$ ):** the proportion of total phenotypic variation within a population that is a result of additive genetic variation.

**Heterozygosity:** a measure of genetic variation based upon the expected proportion of individuals in a population that are heterozygous.

**Hysteresis:** when a perturbed system does not return to its original state after alleviation of the forces that caused the perturbation.

**Metapopulation:** a collection of spatially separated subpopulations that experience some gene flow among them.

**Mixed-stock analysis:** estimation of the contribution of individual local populations to a mixed harvest using the genotypic frequencies from the mixed harvest along with baseline genotypic data from the contributing local populations.

**Neutral loci:** loci that do not affect the fitness of individuals, so that all genotypes have the same fitness.

**Phenotypic plasticity:** variation in the phenotype of individuals with similar genotypes as a result of differences in environmental factors during development.

**Population:** broadly used to mean any collection of one or more local breeding units.

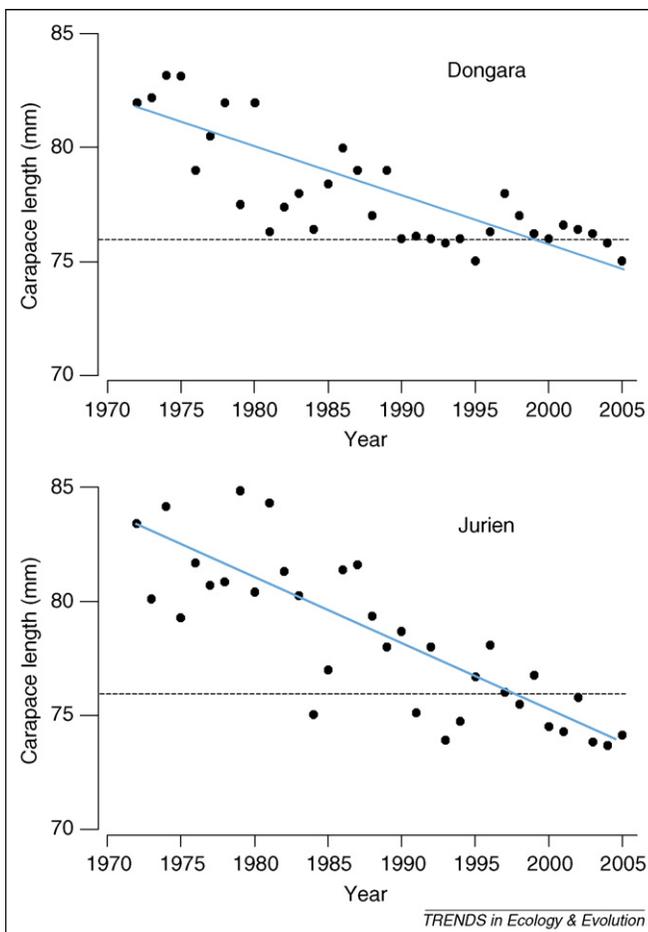
**Probabilistic maturation reaction norms (PMRN):** a function determining a size-specific maturation probability for individuals of a given age.

**Subpopulation:** local groups of individuals within a population that generally mate at random and are delineated by reduced levels of gene flow with other such groups.

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Most of the concern in the literature about genetic changes caused by exploitation has focused on marine and freshwater finfish populations and hunted ungulate populations. However, an incredible variety of wild animal populations are exploited by humans: terrestrial game birds, waterfowl, whales, snakes, turtles, land snails, a wide range of marine invertebrates (anemones, sea urchins, sponges, sea cucumbers, jellyfish), marine birds, kangaroos, forest primates and so on. The same concerns of genetic change elicited by harvest apply to all of these species. For example, the size at sexual maturity in rock lobsters *Panulirus cygnus* off the west coast of Australia has declined substantially over the past 35 years (Figure 1) [10]. This change apparently is partially an evolutionary response to extremely high annual exploitation rates of adults (~75%), combined with a required minimum carapace length of 76 mm in harvested animals.

Understanding the genetic changes and evolutionary responses of exploited populations is crucial for the design of management aimed at sustainable exploitation of natural biological resources [4]. Our primary purpose is to review evidence for genetic effects of harvest in animals and to consider how these might be accounted for in the development of management plans. We also outline



**Figure 1.** Observed decline in mean carapace length of rock lobsters captured in the fishery at two locations off the coast of Western Australia from 1972 to 2005 [10]. Only animals with a carapace length of greater than 76 mm (dotted line) can be legally harvested. This decline apparently is partially an evolutionary response to extremely high annual exploitation rates of adults (~75%), combined with a required minimum carapace length of 76 mm in harvested individuals.

future research needs to advance our understanding of harvest-induced genetic change.

### Alteration of genetic subdivision

Virtually all species have separate local breeding groups (subpopulations) that are somewhat reproductively isolated. Harvest of wild populations can perturb genetic subdivision among populations within a species and reduce overall productivity. The primary problem is that harvesting a group of individuals that is a mixture of several subpopulations can result in the extirpation of one or more subpopulations. This will not be recognized unless the subpopulations are identified separately and individuals from population mixtures are assigned to subpopulations.

Extirpation of some subpopulations is likely to directly reduce overall productivity. In addition, Hilborn and colleagues have shown that productivity of subpopulations of sockeye salmon *Oncorhynchus nerka* can change dramatically over time as environmental conditions change. Therefore, ensuring long-term productivity depends on conserving all subpopulations, including the less productive ones [11]. In addition, reduction in the size or density of subpopulations might decrease the number of migrants among subpopulations and cause increased genetic drift and loss of genetic variation. Harvest can also increase the rate of gene flow into certain subpopulations and cause genetic swamping and loss of local adaptations. An understanding of this population genetic substructure at different points of the life history of a species is necessary to predict the potential effects of harvest on genetic subdivision.

To manage populations sustainably, we need to know what constitutes the harvested population and how it is genetically delineated [12,13]. If the harvested population is part of a wider geographical area connected by migration, then any effects of selective harvest might affect a larger geographical area than anticipated. For example, current sizes of breeding populations of hawksbill sea turtles *Eretmochelys imbricata* in the Caribbean Sea are estimated to be on the order of 1% that of pre-exploitation levels [14]. The government of Cuba has argued that hawksbill turtles found in its waters are part of a closed system, and has sought permission from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to harvest 500 turtles a year in perpetuity. However, molecular genetic analysis of hawksbills collected on foraging grounds indicates that the harvest of turtles in Cuban waters would have potentially harmful effects on nesting colonies throughout the Caribbean because many turtles that breed outside of Cuba would be captured [14].

Harvest of mixed populations is common in migratory waterfowl, marine mammals, ungulates and many other species. For example, Pacific salmon *Oncorhynchus* ssp. are generally harvested in the ocean in mixed stocks that comprise many reproductively isolated subpopulations that spawn in freshwater [11]. Understanding which subpopulations are contributing to the harvest is essential to avoid that some local subpopulations are over-harvested and extirpated while others experience very little harvest whatsoever (Box 1).

### Box 1. Phenotypically selective harvest within and among local subpopulations

Phenotypically selective harvest of mixed populations composed of individuals from many contributing subpopulations can result in both exploitative selection within subpopulations and differential intensity of harvest on subpopulations. For example, hundreds of reproductively isolated local subpopulations of sockeye salmon *Onchorhynchus nerka* contribute to the Bristol Bay fishery in Alaska [11]. There is a gillnet fishery in Bristol Bay that harvests these subpopulations before the salmon return to their home spawning grounds in freshwater. This mixed-stock fishery has the potential to harvest selectively depending upon run timing, body size, body shape and life history (primarily age at sexual maturity).

Quinn and colleagues [64] examined daily records in two fishing districts in Bristol Bay for evidence of temporally selective harvest over a 35 year period. They found that earlier migrants experienced lower capture rates in the fishery than later migrants. As expected, the timing of the run has gotten earlier over this period in response to selection favoring individuals (and subpopulations) that arrive earlier. This observed phenotypic change apparently results from both genetic changes within subpopulations, resulting in earlier run timing of individuals, and differential intensity of harvest on different subpopulations that has favored earlier-arriving subpopulations.

The gillnet fishery also results in selection within subpopulations and differential intensity of harvest on subpopulations because the effectiveness of gillnets in capturing migrating fish is dependent upon body size and shape [65]. Fish that are too small are able to escape by swimming through the mesh, and fish above the target size-class are too large to be wedged in the mesh. Therefore, capture by gillnets is likely to be selective on age at sexual maturity, size at age of sexual maturity and body depth. Subpopulations that spawn in different habitat types show consistent differences for all of these characteristics [64]. For example, males from lake-spawning populations generally have much deeper body depth than males from subpopulations spawning in streams.

To determine the relationship between morphology and fitness caused by selective capture in gillnets, Hamon and colleagues [65] compared harvested fish with fish that escaped the fishery and returned to the spawning grounds. They found that the effects of gillnet selectivity within subpopulations was strongly influenced by variability in age at reproduction. Subpopulations with mixed-aged fish at maturity experienced disruptive selection, with smaller and larger fish having the greatest fitness. By contrast, subpopulations predominantly of a single age-class experienced directional selection favoring smaller fish. In addition, differences in morphology among subpopulations resulted in large differences in harvest intensity. Some subpopulations experienced virtually no fishing mortality, whereas others sustained high mortality due to harvest (>70%).

Extirpation of subpopulations caused by over-harvest has been observed in both marine and freshwater fish [15,16]. For example, the number of streams contributing substantially to production of four salmon species in southern British Columbia suffered a severe decline between 1950 and 1980 [17]. In general, the subpopulations that are less productive and the least resilient to exploitation have been the first to disappear [18]. Moreover, stocks with the most desirable characteristics often experience the greatest exploitation. For example, 'siskowet' lake trout *Salvelinus namaycush* that were prized for their high fat content were the first subpopulation to disappear from Lake Michigan [15].

Exploitation can also increase gene flow or hybridization among subpopulations and potentially swamp local adaptations. Overexploitation could reduce the density of local subpopulations and allow for more immigration from

nearby subpopulations less affected by exploitation. This could bring about the genetic swamping of the remnants of exploited subpopulations and thereby reduce fitness. Recent studies of red deer *Cervus elaphus* report that a change of fine-scale genetic structure appears to be associated with changes in harvest management [19,20].

Examination of genetic samples collected over time (i.e. genetic monitoring) is the most powerful way to detect genetic changes caused by harvest. For example, the Flamborough Head population of North Sea Atlantic cod *Gadus morhua* apparently went through a decline in genetic variation followed by genetic swamping between 1954 and 1998, based upon genetic variation at three microsatellite loci using otolith samples archived over this period [21]. Genetic diversity declined between 1954 and 1970, indicating reduced effective population size apparently resulting from harvest. Genetic variation increased after this period because of increased immigration during a period of exceptionally high exploitation. Thus, the original genetic characteristics of the Flamborough Head population have been lost [21].

### Loss of genetic variation

Reduced population size due to harvesting can also reduce the number of migrants and cause the loss of genetic variation within subpopulations. Genetic variation is measured in two primary ways: heterozygosity and allelic diversity. Loss of genetic variation can reduce productivity of exploited populations both by reducing individual fitness in the short term (primarily affected by heterozygosity) and by reducing the ability of subpopulations to evolve in the future (primarily affected by loss of allelic diversity) [22]. Heterozygosity often is the preferred measure because it is proportional to the amount of genetic variance at a locus (i.e. heritability), and it lends itself readily to theoretical considerations of the effect of population size on genetic variation. Nevertheless, heterozygosity has the disadvantage of being relatively insensitive to the effects of population bottlenecks, so that substantial allelic diversity can be lost even in populations that experience little loss of heterozygosity [23].

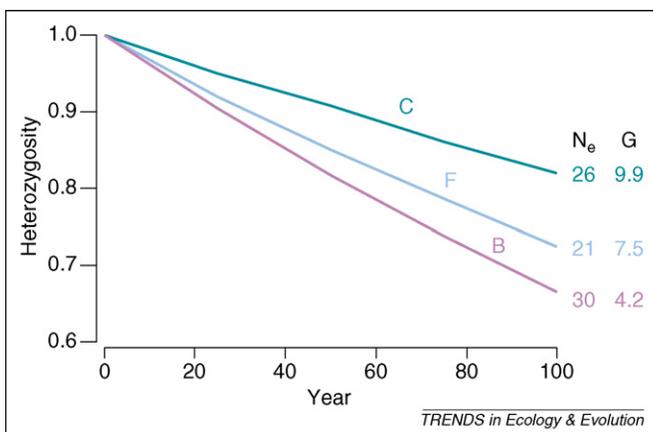
The rate of loss of heterozygosity in each generation as a result of genetic drift is measured by the effective population size ( $N_e$ ). The magnitude of  $N_e$  is determined by demographic factors including  $N_C$  (census population size), sex ratio and the mean and variance of lifetime number of progeny produced by males and females [24]. Harvest often targets specific sex or age classes and thereby can reduce the effective population size and increase the rate of loss of genetic variation. This effect is often exacerbated by ongoing habitat loss resulting in decreased population size and greater isolation. Many recent papers report reduced levels of genetic diversity in a wide variety of exploited species (Table 1).

Management operates in calendar time (e.g. years), whereas knowing  $N_e$  allows the prediction of the loss of heterozygosity per generation. In many species, the generation interval ( $G$ ) is not known and cannot be readily estimated because some of the information required is not available (e.g. reproductive success of males over their entire lifetime). When considering loss of variation over

**Table 1. Examples of loss of genetic variation in exploited populations**

Species	Observation	Refs
African elephant ( <i>Loxodonta africana</i> )	Intense hunting in the early 1900s combined with slow post-bottleneck recovery and lack of gene flow into Addo Elephant National Park (South Africa) is associated with reduced microsatellite heterozygosity and allelic diversity. By contrast, the Krueger National Park population recovered faster owing to immigration after a similar hunting-induced bottleneck and has nearly double the heterozygosity and allelic diversity.	[79]
Arctic fox ( <i>Alopex lagopus</i> )	The Arctic fox population in Scandinavia probably numbered 10 000 historically, but heavy hunting pressure associated with a profitable fur trade in the early 20th century rapidly reduced the population to a few hundred individuals. Analysis of ancient DNA revealed that this population has lost ~25% of the microsatellite alleles and four out of seven mtDNA haplotypes.	[80]
New Zealand snapper ( <i>Pagrus auratus</i> )	Microsatellite heterozygosity and alleles per locus declined between 1950 and 1988 after commencement of a fishery on this population, in spite of an estimated standing population well over 3 million fish.	[29]
Sea otter ( <i>Enhydra lutris</i> )	Analysis of ancient DNA reveals that all the current populations examined exhibit considerably lower heterozygosities at microsatellite loci than samples predating the population size bottleneck caused by extensive fur trading in the 18th and 19th centuries.	[81]
Sika deer ( <i>Cervus nippon</i> )	Three out of seven mitochondrial DNA haplotypes in Hokkaido, Japan, were lost during a 200 year bottleneck caused by heavy hunting reinforced by heavy snow in two winters.	[82]
Tule elk ( <i>Cervus elaphus nannodes</i> )	The Tule elk of the Central Valley of California, USA, dwindled in 50 years from about half a million down to fewer than 30 animals in 1895 through habitat loss, hunting and poaching set about by the Gold Rush. Approximately 60% of heterozygosity was lost, and the present population exhibits little genetic variation.	[83]
Red deer ( <i>Cervus elaphus</i> )	Deer in both open and fenced hunted Spanish populations have lower levels of microsatellite heterozygosity than deer from protected areas.	[84]
White seabream ( <i>Diplodus sargus</i> )	Mediterranean populations in areas protected from fishing have significantly less microsatellite allelic richness than those from nonprotected areas.	[85]

calendar time, a small  $N_e$  might be compensated by a large  $G$  and vice versa. Therefore, consideration of the effects of management on loss of genetic variation over time should not be restricted, as they often are, to  $N_e$  alone because effects of  $G$  are equally important. For example, Ryman *et al.* [25] found that different harvest regimes for moose *Alces alces* can have strong effects on both effective population size and generation interval. Populations with smaller  $N_e$  tended to lose heterozygosity at a slower rate because those effects of hunting that reduced  $N_e$  (e.g. harvesting young animals) also tended to increase the generation interval. That is, hunted populations with relatively smaller  $N_e$  and longer generation interval would lose genetic variation over time (not generations) more slowly than some populations with large  $N_e$  and shorter generation interval (Figure 2).



**Figure 2.** Expected decline of heterozygosity under three different sets of regulations in a population of moose in Sweden with a census size of 100 adults following hunting season [25]. The effective population size and generation interval for each hunting regime is indicated on the right. In hunting regime B, all adults experience identical mortality rates, but calves (less than 1-year-old) are protected and are not hunted. In C, only calves are hunted. In F, adult females with calves are protected so that the risk of mortality of an adult female is reduced as a function of the number of calves (0, 1 or 2) with her at the beginning of hunting season. The regime (B) with the largest  $N_e$  is expected to lose heterozygosity at nearly twice the rate of the regime (C) with a smaller  $N_e$  that has a longer generation interval.

Harvest regulations can reduce the  $N_e:N_C$  ratio and thereby increase the rate of loss of heterozygosity without having any detectable effect on population size. Male-biased, or male-only, harvest is practiced in many species of ungulates and some marine crustaceans (e.g. lobsters), and a skewed sex ratio among breeders might severely reduce effective population size [26]. In addition, harvest regulations can also increase the variance in reproductive success. For example, female brown bear *Ursus arctos*, moose and wild boar *Sus scrofa* are protected by regulations in Sweden when accompanied by subadults. These policies will result in the individuals surviving the hunting season being more closely related than expected by chance, thereby further decreasing  $N_e$ .

Marine fish and invertebrates generally have much larger census and effective population sizes than terrestrial vertebrates [27,28]. However, heterozygosity can be lost even in populations with large census population sizes because  $N_e$  is often much smaller than the census size in many marine species [27]. For example,  $N_e$  in New Zealand snapper *Pagrus auratus* was estimated to be ~100 based on monitoring loss of heterozygosity and temporal changes in allele frequency (Table 1) [29]. The minimum estimated population size during this period was 3.3 million fish; thus,  $N_e:N_C$  was on the order of 0.0001. These results support the conclusion that the  $N_e:N_C$  ratio might be extremely small in a variety of marine species [30]. This suggests that even very large exploited marine fish populations might be in danger of losing genetic variation.

Loss of allelic diversity might have harmful effects in large exploited marine populations where the loss of heterozygosity due to harvest is minimal [22]. Allelic diversity is more sensitive than heterozygosity to dramatic reductions in population size, and  $N_e$  is a poor predictor of the rate of loss of allelic diversity. That is, populations with the same  $N_e$  can lose allelic diversity at very different rates [31]. The reason for this effect is that allelic diversity is affected not only by  $N_e$  but also by  $N_C$  (Equation 9.6.13 in Ref. [32]). Thus, reducing  $N_C$  from, for example, millions

down to thousands might have no effect on heterozygosity, but could result in a decline in allelic diversity [22]. By contrast, greater harvest of males through hunting in ungulates could have limited effect on allelic diversity while reducing heterozygosity because  $N_C$  (e.g. female numbers) can remain large even when  $N_e$  is reduced owing to increasingly skewed sex ratios favoring females [33].

The loss of genetic variation will also be influenced by gene flow among subpopulations that comprise a metapopulation. Estimating the effective population size of a metapopulation is extremely complex [34]. In addition, harvesting might have unexpected effects on the overall  $N_e$  of a metapopulation. For example, Hindar and colleagues have found that small subpopulations within a metapopulation of Atlantic salmon *Salmo salar* contribute more per spawner to the overall effective population size than large subpopulations, and harvesting of the subpopulations jointly in mixed-stock fisheries has a relatively larger demographic effect on small than large populations [35].

### Exploitative selection

Selective genetic changes within subpopulations resulting from exploitation are inevitable because increasing mortality will result in selection for earlier maturation even if harvest is independent of phenotype [5]. Moreover, harvesting of wild populations is inevitably phenotypically nonrandom [5]. That is, individuals of certain phenotypes (e.g. sizes or behaviors) are more likely than others to be removed from a wild population by harvesting. Such selective harvest will bring about genetic changes in harvested populations if the favored phenotype has at least a partial genetic basis (i.e. is heritable). In addition, such changes are likely to reduce both the frequency of desirable phenotypes (Box 2) and productivity.

We use the term ‘exploitative selection’ for the process of selection resulting from human harvest. The term is analogous to ‘artificial selection’ used by Darwin for the intentional selection of certain traits in domestic animals and plants. Rapid genetic change in response to strong selection has been called ‘contemporary evolution’ [36]. However, this term can be misleading because evolution is more than just change by natural selection. Thus, loss of genetic variation caused by genetic drift or increase in genetic variation caused by hybridization would also represent contemporary evolution.

The rate of genetic change by exploitative selection depends upon the amount of additive genetic variation for the trait (heritability):

$$R = H_N S, \quad [1]$$

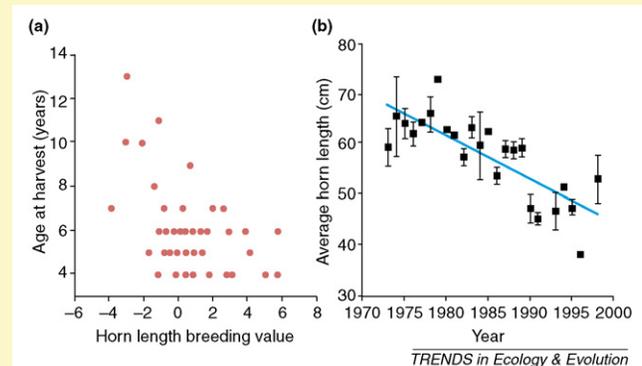
where  $H_N$  is the narrow-sense heritability,  $S$  is the selection differential (the difference in the phenotypic means between the selected parents and the whole population) and  $R$  is the response (the difference in the phenotypic means between the progeny generation and the whole population in the previous generation) [32]. In the case of exploitative selection,  $S$  will be affected both by the intensity of harvest (the proportion of the individuals harvested) and the phenotypic selectivity of the harvest.

### Box 2. Effects of trophy hunting

Trophy hunting (and fishing) targets individuals with certain desirable phenotypes [66]. The result is increased mortality and reduced fitness of those individuals with desirable phenotypes. Consequently, phenotypes that are considered desirable will decrease in frequency. For example, populations of bighorn sheep *Ovis canadensis* are often managed to provide a source of large-horned rams for trophy hunting [67]. In one population of bighorn sheep at Ram Mountain, Alberta, Canada, a total of 57 rams were harvested under such an unrestricted management regime over a 30 year period [67]. This corresponded to an average harvest rate of ~40% of the legal-sized rams in a given year, with the average age of a ram at harvest of 6 years. Because rams in this population do not generally reach their peak reproductive years until 8 years of age [67], hunters imposed an artificial selection pressure on horn size that had the potential to bring about genetic change, provided that the horn size was heritable.

The heritability of horn size, or any other quantitative trait, can be estimated using pedigree information [60]. Mother–offspring relationships in the Ram Mountain population were known through observation, and father–offspring relationships were determined using microsatellites for paternity and sibship analyses [67]. An ‘animal model’ analysis (named as such because it estimates the expected genetic ‘breeding value’ [twice the expected deviation of an individual’s offspring from the term population mean for the trait being considered] for each individual animal in the population) was conducted, which uses relatedness across the entire pedigree to estimate narrow-sense heritability. Horn length was found to be highly heritable ( $H_N = 0.69$ ) [67].

The examination of individual breeding values revealed that rams with the highest breeding values were harvested earliest (Figure 1a) and therefore had lower fitness than rams of lower breeding value [67]. As a consequence, the average horn length observed in the population has steadily declined (Figure 1b). Unrestricted harvesting has therefore resulted in a decline in the trait that determines trophy quality (i.e. horn length) by removing desirable rams of high genetic quality before their reproductive peak.



**Figure 1.** (a) Breeding value (twice the expected deviation of an individual’s offspring from the term population mean) for horn length of trophy-harvested male bighorn sheep at Ram Mountain. Males with greater breeding value are harvested at a younger age and thus tend to have lower fitness than males with lower breeding value [67]. (b) Plot of mean ( $\pm$ SE) horn length of 4-year-old rams over a 30 year period showing the decline of mean horn length in this population.

There are many examples in the literature of phenotypic changes in exploited populations that might be the result of exploitative selection (Table 2). However, it has been difficult to determine whether observed phenotypic changes over time indicate genetic change or are caused by other factors such as relaxing density-dependent effects on growth due to reductions in population density, or abiotic factors such as temperature affecting growth and development [37]. A recent review in this journal critically

**Table 2. Examples of phenotypic changes that could have resulted from exploitative selection**

Species	Trait(s)	Observation	Refs
African elephant ( <i>Loxodonta africana</i> )	Tusks	An increase in the proportion of tuskless females from 10.5% in 1969 to 38.2% in 1989 was directly attributed to illegal hunting in South Luangwa National Park, Zambia.	[86]
American plaice ( <i>Hippoglossoides platessoides</i> )	Body size, age at maturation	Three fish stocks with historically different levels of exploitation showed the same long-term shift toward maturation at younger ages and smaller sizes. This situation warrants further investigation to determine whether these stocks are truly demographically and genetically independent.	[87,88]
Atlantic cod ( <i>Gadus morhua</i> )	Body size, age at maturation, growth rate	Survey data before the collapse of the fisheries in 1992 showed a significant genetic shift toward earlier maturation and at smaller sizes. PMRNs were used to account for any confounding effects of phenotypic plasticity. In the 1970s, fishing selection targeted slow-growing individuals; later, in the 1980s, the net mesh size was increased, resulting in a bigger catch of large, faster-growing individuals. Application of a quantitative genetic model showed a reduction of length-at-age between cohorts of offspring and parents as a result of exploitative selection.	[9,89]
Atlantic salmon ( <i>Salmo salar</i> )	Time of spawning, body size	Earlier-running fish experienced greater harvest by anglers. Allozyme and mitochondrial DNA data from four populations in Spain showed that the late-running individuals which escaped harvest were genetically distinct and significantly smaller. Catch records in Ireland extending back many decades and recent electronic counter data show a reduction in the abundance of early migrants and a decline in size of late migrants.	[90,91]
European grayling ( <i>Thymallus thymallus</i> )	Age at maturation	Gillnet fishing is suggested to have caused a constant reduction in the age and length at maturity in separate populations founded from the same common ancestors.	[92]
North Sea plaice ( <i>Pleuronectes platessa</i> )	Age at maturation, body size	The reaction norms for age and length at maturation showed a significant trend toward younger age and shorter body length.	[93]
Northern pike ( <i>Esox lucius</i> )	Body size	Over a period of four decades, selective harvesting targeted large individuals and directional natural selection favored large body size. The result of these two opposing forces is stabilizing selection, but with a reduction in overall fitness.	[94]
Red kangaroo ( <i>Macropus rufus</i> )	Body size	Hunters target the larger individuals in a group and there is evidence that average size has declined.	[95]

evaluated the observed evidence for a genetic basis of such phenotypic change [38]. **Box 2** provides an excellent example of disentangling the sources of phenotypic change to demonstrate effects of exploitative selection on horn length in bighorn sheep.

Many harvest regimes of fish and wildlife selectively remove larger individuals. Life-history theory predicts that this should select for maturation at a younger age and smaller size [3,39]. This prediction is concordant with the long-term trend toward earlier maturation that has been observed for many commercially exploited fish stocks [39]. However, such trends might also be explained by phenotypic plasticity as a direct response to decreased population size, or by long-term environmental changes.

Probabilistic maturation reaction norms (PMRNs) [40] have been used to help disentangle genetic from plastic effects on maturation [41]. Reconstructing PMRNs from historical data in exploited populations has provided evidence for fishery-induced selection. However, some [42] have argued that because PMRNs do not fully account for physiological aspects of maturation, the observed shifts might reflect directional environmental effects on maturation rather than genetic changes. It is impossible in most circumstances to completely disentangle genetic and plastic effects. Nevertheless, the use of PMRNs provides a useful method to determine whether genetic effects are at least partially responsible for an observed change over time.

### Management and recovery of exploited populations

The most difficult political and economic decision in harvest management is to reduce the current catch to increase the likelihood of long-term sustainability. This decision is especially difficult when taking actions to halt or reverse

historical declines will come at the cost of economic hardship for dependent communities [43]. Management measures to reduce harmful long-term genetic effects are most likely to be adopted by managers if they also help to meet short-term management objectives. For example, maintaining large, old individuals within populations provides both short- and long-term benefits [5,44].

The emphasis on disentangling genetic and plastic mechanisms of phenotypic change is crucial from a basic scientific perspective, but is less important from a strictly management perspective. It is not necessary to prove that an observed phenotypic shift in a wild population is an evolutionary response to harvest to apply evolutionary principles to management. Moreover, complete disentanglement of genetic and plastic responses will seldom be possible, except in laboratory experiments (but see **Box 2**), which have limited applicability to management of harvested wild populations [45]. We recommend assuming that some genetic change due to harvest is inevitable and to apply basic genetic principles combined with molecular genetic monitoring to develop management plans for harvested species. This approach can be especially powerful if archived samples that have been collected over time are available for analysis. Such archived samples are available for many species of fish (scales and otoliths), ungulates (bones and skin) and birds (feathers and skin).

The molecular genetic analysis examination of samples collected over a period of time has tremendous untapped potential to inform and guide management of exploited populations. Genetic monitoring [46] can provide a window into the past, as the examples of genetic swamping of the Flamborough Head population of North Sea cod [21] and the loss of genetic variation in New Zealand snapper illustrate [29]. Analysis of contemporary samples alone

would not have uncovered these important consequences of past exploitation.

### Subdivision

The importance of individually managing reproductively isolated populations is obvious and has long been recognized in fisheries [47]. Nevertheless, application of this understanding is often complex and has proven difficult (Box 3). For example, the concept of fishing the maximum sustainable yield was developed to ensure long-term sustainability. However, if applied to a mixed-stock fishery, this policy is likely to result in a ratchet-like loss of the less productive local reproductive subpopulations [48].

#### Box 3. Use of candidate gene loci to detect genetic subdivision in marine fishes

Knowledge of the breeding structure of fish stocks is crucial for developing and implementing effective management strategies that are urgently needed to maintain sustainable fisheries [56]. However, population genetic studies of marine fishes generally have failed to detect genetic differences even between apparently geographically isolated subpopulations for which there is evidence of some reproductive isolation [27]. This failure results from the large population sizes and high gene flow among stocks of many marine fishes [27]. Even very low exchange rates among stocks with large population sizes will be sufficient to eliminate genetic evidence of population differentiation at so-called neutral genetic markers that are not influenced by natural selection [13].

Recent advances in molecular genetics and statistics allow discovery of regions of the genome influenced by natural selection that can result in substantial genetic differentiation and the ability to identify reproductively isolated stocks. Promising results from salmon have found that genes with known important functions show greater divergence ( $F_{ST}$ ) among spawning populations than neutral genetic markers [68]. The amount of divergence at neutral loci is determined primarily by the absolute number of migrants (e.g. five per generation), whereas the amount of divergence at selected genes is also affected by the proportion of exchange among subpopulations and the local  $N_e$  [13]. Therefore, we expect that differences in divergence at selected versus neutral regions will be even greater in marine species than in salmon because of the much larger local population sizes in marine fishes; greater  $N_e$  allows selection to be more efficient because of the reduced genetic drift in larger populations.

For example, almost no genetic differentiation ( $F_{ST} = 0.003$ ) was found at nine neutral microsatellite loci in Atlantic cod, but substantial differentiation ( $F_{ST} = 0.261$ ) was found at the *Pan I* locus [69], which previous studies have shown to be under natural selection [70]. Recent analysis has suggested that *Pan I* allele frequencies are influenced by temperature, salinity and depth [71]. The utility of divergent markers such as this for stock analysis would be greatly reduced if such differences were not stable and changed over a few generations. Fortunately, comparison of current patterns of genetic differentiation using otoliths going back up to 69 years demonstrated that these allele frequency differences have been stable and therefore can be used as a reliable marker for stock identification [72].

A similar result has been found with European flounder *Platichthys flesus*. Little genetic differentiation was found among subpopulations at nine microsatellite loci ( $F_{ST} = 0.02$ ). However, substantial differentiation ( $F_{ST} = 0.45$ ) was present at a heat-shock locus (*Hsc70*) which was selected as a candidate gene because of its known function [73].

Population genomic approaches allow us to identify genes involved in adaptive traits without prior information about which traits are important in the species in question. These adaptive genes can then be employed to describe spatial genetic structure for species in which neutral genetic markers have not been informative.

There are two main approaches to this problem: first, subpopulations can be harvested individually, and second, genetic monitoring can be used to determine the contribution of each subpopulation to a mixed harvest. Genetic analysis of such mixed harvests can provide rapid and accurate estimates of the contribution of different subpopulations [49,50]. For example, samples of Bristol Bay sockeye salmon (Box 1) are analyzed shortly after capture in a test fishery, and the results of mixed-stock analysis are radioed to the fleet every other day so that harvest effort can be adjusted (J.E. Seeb, pers. commun.) [51].

### Loss of genetic variation

Small populations are most likely to be affected by the loss of genetic variation due to excessive harvest because of their smaller effective population size. Management actions that reduce effective population size below threshold values where loss of genetic variation might have harmful effects should be avoided. As we have seen, substantial loss of genetic variation can occur even when census population sizes are very large because the genetically effective population size is often much smaller than the census size in many harvested species of marine fishes and invertebrates. The only way to detect such 'cryptic' loss of genetic variation of exploited populations is empirical observation of genetic variation over time. Genetic monitoring programs can provide a powerful means to detect loss of genetic variation if enough marker loci are used [21,28,29,33,46] (Box 4).

### Exploitative selection

The amount of genetic change caused by exploitative selection is a function of the intensity of harvest and the phenotypic selectivity of the harvest (Equation 1) and is furthermore related to the effective population size. Lowering rates of exploitation is the most direct way to reduce the effects of exploitative selection. Consideration should also be given to management approaches that spread the harvesting across the distribution of age and size classes, or target intermediate-sized individuals by establishing an upper size limit on individuals (especially for long-lived species). These actions will both reduce the long-term effects of exploitative selection and increase the number of older females that produce more and higher-quality offspring in the short term [5,44]. However, upper size limits might reduce  $N_e$  because individuals surviving to the size where they are 'safe' will contribute a disproportionately large number of progeny, and this is expected to increase the variance of family size [25]. This effect on  $N_e$  might be substantial in some cases depending on the age distributions before and after introducing the limit [25]. However, the expected effect on heterozygosity over calendar time would be more complicated because this harvest strategy could also lead to longer generation interval.

The effects of selection can sometimes be reduced by harvesting fish after reproduction by changing either the time or location of harvesting. For example, the northeast Arctic stock of Atlantic cod uses the Barents Sea for feeding but spawns further south off the northwest coast of Norway [52]. Harvesting on breeding grounds in the Barents Sea rather than feeding grounds would avoid removing young

#### Box 4. Outstanding questions

##### How can we best monitor for genetic effects of harvest and exploitative selection in wild populations?

This question is extremely important because early detection of potentially harmful genetic change will maximize our ability to implement management to limit or reverse the effects before substantial or irreversible changes occur [53]. Recent molecular and statistical tools make genetic monitoring increasingly feasible and cost effective. Thus, there is enormous untapped potential for genetic monitoring with population genomic approaches [61] to detect and avoid detrimental genetic effects of harvest and exploitative selection [33]. This is true for many harvested populations [21,28,29]. We propose that genetic monitoring of valuable exploited populations should become a standard management tool. Genetic monitoring can provide crucial demographic information [46], as well as provide a warning about the loss of genetic variation or the response of key regions of the genome to exploitative selection. Genetic monitoring will be especially valuable if historical samples are available to provide a window into the past.

##### How can no-take areas best be designed to mitigate the detrimental effects of exploitative selection?

Increased efforts need to be applied to the development of alternative management approaches to design areas that will protect a broad representation of genetic variation within open populations [5,7]. Crucial information for the design of geographical reserves includes the appropriate size of populations in non-harvested areas and the rate of gene flow and dispersal between areas [57–59]. A temporally variable reserve design could also be considered, where harvesting is conducted only in some years or time periods.

##### What have been the ecological effects of exploitative selection on non-target species arising from altered community interactions, and what will be the ecological consequences of restoring historical population phenotypic means and population sizes?

Reduced population sizes and smaller size at maturity of harvested species will inevitably affect the community interactions involving other species [74,75]. When the target species plays a key role in the food web, the effect are potentially considerable, with cascading and unexpected impacts such as prey shifts, altered predator–prey and other trophic dynamics [76]. State shifts have been observed as a result of suppression of predation pressure upon sea urchins, leading to drastic overgrazing of macroalgal forests and resulting in vast ‘urchin barrens’ [77]. Predicting where and when state changes such as these might occur is difficult. Conversely, release of predation pressure in marine reserves has been shown to reverse this effect [78]. If management of targeted species reverses declines in exploited species, how will ecosystems respond? Will the restoration be straight forward and predictable, or will hysteresis effects complicate prediction?

fish before they can reproduce. By contrast, harvesting on the feeding grounds would select for early maturation because late-spawning fish might be harvested before they mature. However, there are challenges in making this biological solution socially palatable because of its potential economic impact on the fishing fleet and markets through increased seasonality of harvest and supply [52].

Recovery following relaxation, or even reversal, of exploitative selection often will be much slower than the initial accumulation of harmful genetic changes [52–54]. This is because harvesting often creates strong selection differentials whereas relaxation of this selective pressure will generally result in only mild selection in the reverse direction. de Roos and colleagues [53] used an age-structured fishery model to show that exploitation-induced evolutionary regime shifts can be irreversible under likely

fisheries management strategies such as belated or partial fishery closure. This effect has been termed ‘Darwinian debt,’ and has been suggested to have general applicability [54]. That is, timescales of evolutionary recovery are likely to be much slower than those on which undesirable evolutionary changes occur. However, gene flow has the potential to accelerate the rate of recovery by restoring alleles or multiple-locus genotypes associated with the trait. For example, trophy hunting might reduce or eliminate alleles for large horn size, but gene flow from national parks with no hunting might quickly restore alleles associated with large horn size.

##### Protected areas

No-take protected areas have great potential for reducing the effects both of loss of genetic variation and harmful exploitative selection. Models of reserves in both terrestrial [55] and marine [56] systems support this approach for a wide variety of conditions. However, the actual effectiveness of such reserves on exploited populations outside of the protected area depends upon the amount of interchange between protected and nonprotected areas and upon understanding the pattern of genetic subdivision [57,58]. It has been suggested that as exploitation pressure intensifies outside protected areas, local protection could select for decreased dispersal distance and thereby increase isolation and fragmentation and potentially reduce the genetic capacity of organisms to respond to future environmental changes [59].

##### Future directions

We face several difficult challenges before we can develop management plans that minimize harmful genetic changes caused by exploitation of wild populations (Box 4). Future developments and application of genomic technology have great potential for addressing these questions and clarifying the effects of harvest and management on wild populations [60]. Such technologies will allow the simultaneous study of hundreds of loci in hundreds of individuals [61]. This will improve our ability to detect changes in population subdivision and genetic diversity resulting from harvest or management actions. Moreover, the continued development of individual-based analytical methods will allow identification of migrant individuals, as well as subpopulations (e.g. management units) without the bias associated with *a priori* grouping of individuals based on geographic or phenotypic similarities [62]. In addition, studies of candidate gene loci with known function can help managers detect adaptive differentiation, subtle or cryptic population subdivision (Box 3) and the genetic effects of management on specific traits (such as body or horn size or growth rate).

Harvest management faces a pressing need to develop analytical tools for interpreting observations, facilitating genetic monitoring and formulating questions. For example, there is great scope to use modeling to predict when selective harvest might cause evolutionary change, and when reversal is expected to be possible under various conditions ( $N_e$ , heritability, dispersal, selection pressure, correlations with reproductive rates, plasticity, etc.). This will allow the development of informed management

guidelines aimed at minimizing exploitative effects of harvest. Similarly, the design of protected areas requires careful consideration and modeling to achieve the intended goals. Key parameters include the actual and effective population sizes of the populations within and outside the protection zone, the amount of exchange between them, and the heritabilities and exploitative selection pressures for appropriate characters. These factors might be widely different for the different species meant to be protected, and they are also expected to show considerable local variation.

### Concluding remarks

Our review has presented evidence from a wide variety of animal species that human exploitation has brought about three types of genetic change in natural populations. There is ample evidence that exploitative selection is at least partially responsible for phenotypic changes over time observed in exploited populations. However, determining the role such changes have played in the decline in harvested populations is much more difficult [37,38]. This issue is analogous to the controversy in conservation biology about the causal role of genetics in extinction [63]. Extinction, or population decline, is always the result of a variety of interacting biological and environmental factors. Attempts to identify a single cause (e.g. loss of genetic variation or genetic change brought about by exploitative selection) in the decline of wild populations are doomed to fail. A more prudent course is to assume that harvest will result in exploitative selection, develop management and recovery programs that will minimize potential harmful effects of genetic changes due to harvest and then to monitor for molecular genetic changes as well as key life-history traits [38].

How do the genetic effects of exploitation differ in the two major groups of exploited species, marine fisheries and terrestrial ungulates? The primary difference is that the effective population size of many marine fish and invertebrates is much larger than the effective population size of terrestrial ungulates. The obvious effect of this is that isolation, fragmentation and loss of genetic variation will generally be a more crucial problem in ungulates. However, an important corollary of this is that the larger effective population sizes of marine populations increase the efficacy of natural selection and increase the likelihood that important local adaptations exist, even where there is little genetic divergence at neutral loci (Box 3).

These are exciting times in the application of genetics to the management and recovery of exploited populations. Genomics is in the process of revolutionizing our understanding of the demographic and genetic connectivity of marine species (Box 3). The integration of our new genetic insights into models and novel statistical approaches, such as PMRNs, will help us delineate boundaries and quantify effective population sizes of local populations, estimate the heritabilities of the traits of concern and evaluate how they affect fitness, and predict the selective changes induced by various exploitative regimes. Finally, the genetic monitoring of samples collected over time will provide a valuable tool for management of exploited populations.

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