Yellowstone Ecological Research Center

May 17, 2023

Dear Interested Person, Party or Organization,

Since the 1990s numerous biologists and NGOs have asked me what effect killing adult coyotes has on the remaining population. In response, you will find (below) my third update to a scientific opinion letter (SOL) I first wrote for Brooks Fahy of Predator Defense to address this question. At the end, you will find a summary showing the 20 effects of coyote-killing in four categories—demographic compensation, behavioral response, changes in culture/society, and ecosystem impacts.

While responses vary, overall the science shows indiscriminate killing to be ineffective and counterproductive. Claims are frequently made that only offending individuals are targeted, and then killed or removed, but there is no verifiable evidence that this is possible, let alone effective. What agencies call "control" is actually indiscriminate killing of adult coyotes, which leads to a higher percentage of females breeding, higher pup production, rapid immigration or replacement of breeding adults, and a myriad of other responses detailed in this letter.

It cannot be over-emphasized how strongly coyote populations compensate for population reductions after indiscriminate killing. In addition to the population responses, the results of coyote-killing include multiple detrimental effects on individual coyotes, packs, species populations, and the entire predator-prey ecosystem due to trophic-level interactions.

OVERVIEW

Because the question at hand is complex, I will present it in a simple scientific and defensible "impact/response" framework where the human *impact* is the removal or killing of adult coyotes—9 months old and capable of breeding—often reported as annual mortality. The reduction in population size is an impact that elicits a population *response* over time, hence a density-dependent response that is possibly compensatory—a rebound back towards the original population size. Such a compensatory response can vary. It could be weak (the population stays close to the level it was reduced to), strong, complete, or even hyper-compensatory where the population rebounds to a higher level than it was before the impact. The timing of the compensatory response can be immediate or slower over several months to several years.

The compensatory response to density reduction due to removal or mortality of adults can be grouped into *demographic*, more at the population level (e.g., average litter size), and *behavioral*, often at the individual level within a pack and can act independent of population demography—for example, a breeding female may move her litter to a safer location after an adult pack member is killed. Thus, this SOL deals primarily with the demographic response at the population and pack (social group) level focusing on two demographic events that are *additions* to the population: (1) the reproduction or better described as *reproductive recruitment* (the number of pups born that survive to the fall population when they are reproductively mature) and (2) immigration at the pack level. There are many behavioral and individual responses that are not included nor addressed in this update. Similarly, there are other alternative factors that affect the demographic response by adults to human-caused mortality (also called exploitation) that are mostly outside the scope of this SOL. For example, the influence of extrinsic factors such as climate and habitat change on wild prey can directly affect intrinsic compensatory responses.

BACKGROUND

The Goals of "Control"

There is a repeated claim that killing coyotes (often referred to as control and/or human exploitation) decreases predation on domestic livestock and game animals such as mule deer or antelope. But before this is addressed, it is important to understand the type of control practices that attempt to reduce predation. Nearly all, if not all reductions, killing, or culling programs, often referred to as *control* practices, are simply indiscriminate killing of adult coyotes. Yet it is often stated that the offending individual (i.e., culprit) is targeted and then killed or removed. In fact, there is a near complete lack of evidence from observations or studies that support this claim and document removal of the offending individual (if any)—let alone the forensic documentation of predation—and show removal of the offending individual to even be effective, especially in social species like coyotes and wolves. Thus, regardless of the compensatory response by coyotes, the inability to verify the removal of the offending individual undermines their claim at the onset. This is why this SOL deals with this type of impact—indiscriminate killing—and does not address the question of whether removal of the offending individual is effective. This SOL also does *not* address the effectiveness of indiscriminate killing in terms of ethical standards nor the impact it has on the ecosystem services provided by coyotes, an apex predator in North America implicated in powerful trophic cascade interactions as first brought forth in a famous paper that looked at the absence of the apex predator, the coyote (Crooks, K.R. and Soule, M.E. 1999. Mesopredator Release and Avifaunal Extinctions in a Fragmented System. Nature 400: 563-566).

Both governmental research (mostly funded and conducted by USDA Wildlife Services) and government-funded research clearly indicate that offending individuals are most often breeding adults, often called the "alpha pair," that provision their pups. There is a strong incentive to kill large packages of prey to feed fast-growing pups that can starve or succumb to other proximate factors (e.g., disease) if they become malnourished. This nutrient incentive (and caloric stress) starts when females are pregnant and are maximized during the summer after weaning and before pups forage on their own in late summer. The early late-May through July period is also, not surprisingly, the period when pup mortality from disease (proximate cause) and starvation (ultimate cause) occurs. Recruitment of pups into the fall breeding population is primarily how coyotes attain genetic fitness.

Because reproduction is almost exclusively performed by the breeding pair (that is nutritionally stressed), the primary goal of 'control' is to reduce the number of *breeding adults* and consequently reduce predation on livestock and wild ungulates. In highly social, territorial species like coyotes and wolves, the *effective population size* is measured by the number of breeding pairs or the number of territories. Thus, to determine the effectiveness of control (human killing) practices, one must know the number of territorial breeding pairs on the landscape both before and after the impact of control which attempts to target one or both breeders within a pair.

There is nothing more conserved, and sought after, by adult coyotes to increase their genetic fitness than to become a territorial breeding adult. Subsequently, this is a fundamental reason that indiscriminate killing is ineffective. With annual mortality rates at, or exceeding, 70% (which is rarely attained and at great costs) the number of breeding pairs remains stable (with the pack size decreased to 2 or 3 individuals). At even higher rates of mortality, it appears that one male can breed with several breeding females as was suggested by (Berg and Chesness 1978), and the number of litter produced is still constant. When food is abundant, a second (beta) female can sometimes successfully breed (produce a litter) within a pack. This was estimated to occur 14% of the time in unexploited populations with pack sizes ranging from 3.4 to 6.2 individuals. The mechanism driving the occurrence of a "double litter" is unknown but is a highly probable response to a surplus of food either within a territory or across a landscape if there are territorial vacancies.

<u>Common Sense and Evolution</u>

It cannot be over-emphasized how strongly coyote populations compensate for population reductions. And I will attempt to explain why that is within a general evolutionary perspective before examining more immediate demographic responses. First off, compensatory or density-dependent responses to exploitation (human-caused mortality) are common in mammals and present in all territorial populations at or near carrying capacity—more clearly described as habitat saturation for non-overlapping territorial species (see Fowler, 1981. Density Dependence as Related to Life History Strategy, Ecology Vol 62: 602-610). Thus, it should come as no surprise that coyote populations have strong density-dependent compensatory responses at or near habitat saturation (few, if any, occupiable territorial vacancies) especially given a locally available surplus of behaviorally suppressed females capable of breeding. In fact, a large majority of adult females are pregnant every year, but usually only dominant females (alphas) successfully reproduce (producing one or more surviving pups).

Second, both evolutionary biology and the results of research (e.g., a 20-year study in Yellowstone National Park before and after gray wolf reintroduction) suggests that the basis of their *demographic and behavioral* resiliency is embedded in their long evolutionary history. That is, coyotes evolved, and learned to coexist, in the presence of larger competitors capable of killing them, namely, and more recently, gray wolves—a dominant competitor and natural enemy that overlapped the historic range of coyotes in North America for tens of thousands of years. Prior to widespread human persecution of predators starting in the mid-nineteenth century, wolves have provided a constant selection factor inflicting mortality, competition, and numerous other sub-lethal effects as revealed by numerous wolf-coyote investigations. Collectively, intense selective pressures by larger competitive species (and now humans) result in a species that has existed in a relatively constant state of colonization with many specialized adaptations. These demographic and behavioral adaptations are numerous and diverse and allow coyote populations to easily overcome the relatively less effective human mortality and control practices compared to the impact of wolves.

Again, the reduction of depredation on domestic livestock (and predation on game animals) due to indiscriminate killing may or may not occur. And while it is incumbent on the perpetrator to justify their environmental impacts (e.g., NEPA), few, if any valid studies, demonstrate the effectiveness of human control practices (see Treves et al. 2016. Predator Control Should Not be a Shot in the Dark. Frontiers in Ecology and the Environment 14: 380-388). Human control (killing) is short-term and intermittent, compared to the sustained presence of wolves, from every day to many thousands of years (24/7/365/1000).

Mechanics of demographic compensation

Thus, there are two main demographic *responses* in coyote populations to the *impact* of killing: (1) an increase in the number of pups surviving to sexual maturity (*reproductive recruitment*), and (2) increased *immigration* that can be immediate or delayed. Reproductive recruitment starts when ova are shed and implanted in territorial breeding females and ends in the fall when pups become reproductively mature adults when about 9 months old. Replacement of breeders is known to readily occur by two mechanisms: (1) immigration of an individual from outside the pack, or (2) internal transition where a non-breeding adult within the pack becomes a breeder (referred to as ascension of a beta to an alpha). Also, it is clear and obvious that killing adults does in fact reduce population density and is required in order to drive the compensatory responses described below. This reduction is often observed as an immediate reduction in pack size. However, it can be difficult to measure if the replacement is immediate from outside the pack.

Overall, an important question is not so much if these mechanisms occur but how strong is the compensatory response (magnitude not mechanism) and does it occur in a way that the annual window of opportunity to produce a litter is missed or not. Thus, the removal of offending individuals may temporarily alleviate predation especially if an annual reproduction (a litter) is lost. If immigration replaces the number of breeding adults so that an annual litter is not lost then the effectiveness of control is probably short-term if at all because of compensatory responses to density reduction. The immigration response time may be immediate compared to the once-per-year chance to reproductively compensate for density-reducing events with an increase in the number of pups produced. Thus, there are measurable short-term and long-term demographic responses that result in the ineffectiveness of control and management practices, and the response to control can result in an increase in predation rates on domestic livestock and game populations. Whether the breeding adults are removed or not, it is likely that at least some compensating responses described below will take place anyway. Again, it’s a matter of magnitude not the mere presence of a mechanism.

Scientific opinion on whether compensatory mechanisms negates the effectiveness of control: The following demographic compensatory responses I describe are based on published research (reviewed up to 1999 in Crabtree and Sheldon, 1999), results of analysis of coyote study populations subjected to various levels of reduction or exploitation, the work I have conducted with coyote populations in three study areas over the past 38 years in Washington (4 years, unexploited population), California (2 years, exploited), and Wyoming (20 year field study of a pre-wolf unexploited population then exploited by wolves after reintroduction in 1995-96). I also attribute my knowledge to my experience as a fur trapper in my college years and a special dog named Chima who was able to communicate to me what her fine-tuned nose was 'seeing'.

There is little, if any, scientific basis to justify control (reduction by killing) programs that indiscriminately target adult coyotes, let alone breeding adults. As with any federal action, the burden of proof should be upon them to demonstrate both the biological and economical effectiveness and justification of their proposed activities (see NEPA). Even the federal agency called Wildlife Services often points out the lack of academic research demonstrating effectiveness. And their research arm has indicated their ineffectiveness. In fact, the mechanisms described below suggest that control (whether selective or widespread) increases the immigration, reproduction, and survival of remaining adult coyotes. In several papers, it has been reported that a sustained reduction of coyote numbers can only be accomplished if over 70% or more of the adults are removed (exploited) on a sustained basis. Review of field research and modeling (including my own) indicates that even with intensive control efforts, this level is rarely, if ever, achieved. And if it is achieved, it is likely to be much more expensive than simply providing monetary compensation for losses. A thorough review and synthesis of coyote ecology and demography can be found in a book chapter (see Crabtree and Sheldon 1999). Actual reduction in the population density (and the number of coyotes) does occur and is primarily a function of smaller pack size for a year or more. Betas, yearlings, and 6- to 9-month old 'pups' killed often constitute the majority of coyotes killed. Reproducing adults or alphas that are older and experienced are killed in a lower proportion than their occurrence in the population and compose less than half of an unexploited or lightly exploited population.

The primary objective of an adult coyote seeking to increase its genetic fitness is to find a territorial opening, pair-bond, defend it, exploit the food resources within, and *successfully reproduce* thereby increasing their genetic fitness. The competition for a territorial vacancy—a breeding adult position—is thus, intense. Overall, this is why control practices rarely reduce the effective population size and subsequently fail to decrease predation on domestic livestock and wild game. Thus, the primary mechanism or lack of a mechanism for compensatory response is as follows:

(1) **Immigration.** This is the most effective and immediate means by which the effective population size rebounds or compensates for indiscriminate killing. There is little evidence that non-territorial loners and beta pack members are replaced. Rather, if breeding adults are killed, they are either replaced immediately or within the next 9 months, especially during the winter when courtship and territories are set up or reinforced with active defense, scent-marking and

vocalizations. Approximately 90% of breeding adults are replaced within the following year. Immediate immigration often occurs within the pack—called internal transition—if a breeding adult is killed in a pack of 3 or more individuals. A surviving beta pack member ascends to the alpha or breeding position. Immigration or replacement of breeding adults is also achieved by non-territorial individuals from outside the pack, especially when both alphas are killed and the pack disintegrates. This is the expected response for a territorial species with surplus (non-breeding) adults and dates back to classic studies of territorial birds following removal of breeding adults involved in courtship and nesting.

(2) **Reproduction and Reproductive Recruitment.** This is a complex series of interactions and I have broken "reproduction" into life history segments as well as a section on the mechanistic basis for why more "pups are produced" when humans indiscriminately kill adult coyotes. Litter size at birth. Coyotes are monestrous which means the breeding, mated pair attempt to produce a litter once per year. Reported litter size at birth is highly variable and may be due in part to the technique used to determine it. Litter size is usually always reported as either the number of placental scars or the observed counts at den sites (when pups are a month old or older). Both methods may be biased because they are either well before or after parturition. Regardless, litter size at birth does not appear to be affected by density-reducing control (killing adults) as previously reported by Crabtree and Sheldon (1999) which is contrary to USDA-funded research. Knowlton (1972) reported an inverse relationship between an unreliable abundance index (number of coyotes per trap line effort) and litter size varying between 4.3 to 6.9 based on placental scars. However, litter sizes reported from den counts varied only from 5.0 to 5.7 pups.

There was no statistical analysis conducted, however, using scars, he inferred litter sizes on 7 counties based on a qualitative assessment of light, moderate, and intensively controlled levels. This study appears to be the basis of the commonly held notion (called a factoid) that litter size at birth increases when populations are exploited. Recently, I compared counts of litter-size-at-birth to concurrent estimates of annual mortality of adults in 14 studies. It resulted in a slope of 'zero' further indicating the fallacy of this assumed mechanistic response. Although high levels of protein intake around the time of ovulation can cause an increase in the number of ova shed and implantation sites, there is no empirical evidence that litter-size-at-birth increases with exploitation (human-caused coyote mortality). Rather, an increase in litter survival (a decrease in the normal high mortality rates of coyote pups during the summer) is the primary compensatory response related to reproduction.

Summer Litter Survival is the key to understanding compensatory reproduction. Human exploitation (killing) reduces the population primarily through a reduction in pack size which results in more pups surviving during the normal high pup mortality (starvation) during summer. In unexploited populations, it is typical for about 2 pups—out of an average litter size of 6—to survive to the fall. A high survival rate of pups from birth to fall when recruitment occurs, can be measured by the number of young-of-the-year in the fall/winter population sample. A high proportion of young-of-the-year is commonly observed among exploited populations where pack size is low (a breeding pair or breeding pair with one adult pup from a previous litter called a helper). In our research first-time breeding pairs produce litters that survive at the highest rates observed. Presumably, first-time breeding pairs have higher fat reserves than packs or pairs that have experienced the costs of reproduction in the previous year.

A simple mechanistic basis for compensatory reproductive fall recruitment is as follows. Density-reduction from human exploitation allows the pups that normally die due to starvation during the summer months in populations, to survive. I believe that the best predictor of compensatory response to the impact of mortality on coyote populations is: **the ratio of the number of territorial adults to the availability of wild prey biomass.** Overall, increases in wild prey populations in the population region, in particular within the confines of the defended territory, can cause an increase in this key factor to understand the mechanism underlying the coyote's often powerful compensatory response. It is further explained below.

This exploitation causing higher pup survival is fundamentally a function of the general mammalian reproductive strategy that delays the majority of reproductive energetic investment beyond the gestation period, the post-partum and neonate state (e.g., young pups). The caloric demand of offspring reaches an apex in May, June, and July when coyote pups grow very fast. Thus, the normal litter of six pups has a good chance of (a) surviving the typically high summer mortality period and, (b) being recruited into the pack the following winter as adults thereby returning the previously exploited population to normal densities. By contrast, in the two unexploited populations I investigated, the average litter size at birth was 5 or 6, but due to high summer mortality, only an average of 1.5 to 2.5 pups survive. In populations subjected to moderate to high levels of exploitation (25% to 70% removal annually), there appears to be an ample number of breeding pairs to occupy all available territory openings with high pup survival rates (more than half of those born survive to adulthood). Compared to an unexploited population, these levels of exploitation can result in a doubling or tripling of the number of hungry pups that need to be fed.

It is strongly suggested that the remaining breeding adults (typical pack size of 2 or 3) now have access to increased food availability within their defended territories and can better provision fast-growing that might otherwise starve. Summer starvation is widely observed in populations with low adult mortality resulting in 2 or 3 pups surviving to the fall when recruited into the breeding population. Thus, surplus food likely improves the nutritional condition of breeding adults, which translates into higher pup birth weights and higher summer pup survival. Remember, alpha male coyotes and associate or beta adults, often female, also help feed pups from May to July. It is no surprise that first time breeders in coyotes and wolves typically have high survival rates in their first litter

Human control resulting in a reduction in the density of the population results in a smaller social group size (i.e., pack) which increases the food per coyote ratio within the defended territory. The food or prey surplus is then biologically available to potentially increase the *production* of more pups either through an increase in litter size at birth or a decrease in the normal high the mortality rate of pups surviving to the fall.

Topics from previous versions of the SOL

(a) **Prey targeting.**
Reductions in coyotes capable of breeding (at 10 months of age) result in smaller pack sizes which leaves fewer adults to feed pups. Although remaining adults may well have access to more prey within their defended territories, this may further add incentive for the remaining adults to kill larger prey such as domestic sheep as well as putting pressure on the adults to select for the more vulnerable prey and venture close to areas of human activity that they otherwise avoid. Because predators like coyotes also learn what is appropriate food when they are pups and are reluctant to try 'new' food sources unless under stress (such as having to feed a large litter of pups), reduction programs, in effect, may be forcing coyotes to try new behaviors (eating domestic livestock) which they would otherwise avoid. Research has clearly shown that higher numbers of adult pack members provide more den-guarding time and more food brought to pups. Without the pressure to "maximize" efficiency in hunting for food for pups, adults provisioning pups may be able to subsist on larger numbers of smaller prey (e.g., rabbits and small rodents) rather than going for livestock or other, larger prey like antelope and mule deer fawns. Although coyotes are exposed to a significant risk of injury when hunting and killing larger prey, larger litter sizes might 'tip the balance' in favor of selecting larger prey and livestock.

Large packages of prey, (such as sheep, as opposed to the more natural and common prey species of voles, mice, or rabbits) make for more efficient sources of nutrition because hunting adults have to invest less energy per unit of food obtained. Research funded by Wildlife Services clearly indicates that the primary motivation to kill domestic sheep is to provide food for fast-growing pups.

(b) **Females breeding**.
Non-selective, indiscriminate killing of adults) cause an increase in the percentage of females breeding. Coyote populations are distinctly structured in non-overlapping but contiguous territorial packs. About 95% of the time, only one female (the dominant or alpha) in a pack breeds. Other females, physiologically capable of breeding, are "behaviorally sterile". Exploitation rates of 70% or higher are needed to decrease the number of females breeding in a given area. Either a subordinate female pack member, or an outside, lone female can be quickly recruited to become an alpha or breeding female. My research has shown that light to moderate levels of reduction can cause a slight increase in the number of territories, and hence the number of females breeding.

(c) **War zone.**
Reduction or removal of coyotes causes the coyote population structure to be maintained in a colonizing state. For example, the average age of a breeding adult in an unexploited population is 4 years old. By age 6, reproduction begins to decline whereby older, alpha pairs maintain territories but fail to reproduce. This may eliminate the need to kill sheep or fawns in the early summer in order to feed pups. Exploiting or consistently reducing coyote populations keeps the

age structure skewed to the younger more productive adults (average age of an alpha is 1 or 2 years). Therefore, the natural limitations seen in older-aged, unexploited populations are absent and the territorial, younger populations produce more pups.

(d) **Delay Dispersal.**
Reductions in adult density of coyotes also cause young adults (otherwise prone to dispersing) to stay and secure breeding positions in the exploited area where there are vacant territories to occupy. This phenomenon is well-documented by research conducted by Wildlife Services and other researchers. Research also indicates that this is the age class most frequently involved in conflicts.

(e) **Alternate prey.**
An aspect of coyote predation on livestock that is often overlooked is the availability, or dearth of alternate prey. Wildlife Services' research has demonstrated that coyotes will avoid novel prey, such as domestic livestock. In addition, it is risky for coyotes to predate upon domestic livestock because of human control actions associated with this behavior. Related research indicates that predators switch to alternative prey when a preferred prey item is absent or in low numbers. Voles and other rodents like jackrabbits are a preferred major staple of coyotes in the West. These prey species require cover and ample supplies of forage (grass and forbs). On many western rangelands grasses, forbs, and protective cover have been greatly reduced by domestic livestock grazing, leaving predators with fewer preferred prey to utilize. Present or historic grazing impacts should be assessed as a likely means of predicting overall predation rates on other prey species, especially prey like domestic sheep, which are already vulnerable to predators due to their lack of anti-predator behaviors.

(f) **Accelerated selection pressures and learned behaviors.**
A relatively unexplored, but promising avenue of research is the long-term genetic and behavioral changes in coyote populations subjected to decades of exploitation. It seems obvious that the type of selection pressures and selection rates have been greatly changed for coyote populations, after a century of exploitation at 20% to 70% per year. More nocturnal, more wary, more productive, more resilient individuals have probably been intensively selected for. This in turn may cause coyote populations to resist control practices that previously were effective. In addition, the possibility of social facilitation and learning may be altered or reduced. Coyotes, like many mammals, learn to habitually use certain prey or habitats from other individuals in the population, especially from older adults in their social group (if they have one). Coyotes, already a highly social and adaptable species, are held in a younger colonizing state when they are exploited and learned or traditional behaviors may be lost. Individuals are therefore more susceptible to learning novel prey sources or trying out novel habitat types and are frequently associated with conflicts such as livestock predation.

(g) **Assessment of Alternatives.**
There are many questions to be answered such as, "How will coyote populations respond once predator reduction or control programs are terminated?" or "Are there other management alternatives, both lethal and non-lethal, that may be effective in reducing predation on domestic

livestock"? "How do economics figure into management options"? This letter and scientific opinion only addresses the narrow, but important topic of the impacts of human-caused reduction or 'control' on coyote demographic parameters. We see little, if any, evidence to justify control practices on an ecological basis. This letter also addresses a long-held belief that human control of coyote populations are 'necessary', similar to 'mowing a lawn' to keep it from growing out of control. This belief has no scientific basis whatsoever. Even research conducted by Wildlife Services reports a variety of factors that keeps the lawn from growing. Their research repeatedly concludes that the primary means of population limitation is territoriality itself, which imposes an upper limit on density (or lawn height). Paradoxically the prevalent use of lethal control by Wildlife Services opens up a 'Pandora's box' of behavioral and demographic responses that negate any long-term effectiveness of control. The predominant responses of coyote populations to lethal control efforts are to: (1) increase the number of pups produced (recruitment), (2) increase immigration into the conflict area, and (3) increase behaviors that further exacerbate the conflict. Collectively, this results in higher predation rates on domestic livestock and wild ungulates.

(h) **The three E yardsticks.**
Coyotes are still products of their evolutionary past. Biological, economical, and ecological evaluation of control practices should be a requirement undertaken before any public or private effort to reduce losses due to coyotes or any other predator. In conclusion, it is my opinion based on decades of field research that the common practice of reducing adult coyote populations on western rangelands are most likely ineffective and likely causes an increase in the number of lambs, fawns, and calves killed by coyotes.

A Summary of the Effects of Exploitation on Predator Populations

The 20 responses listed below are divided into four general categories: (1) demographic compensation, (2) behavioral response, (3) changes in culture/society, and (4) ecosystem impacts. How many of these occur—and their individual magnitudes—will vary by species, the severity and type of control action taken, habitat, season, prey availability, and presence of competing carnivores in the target area. Interactions between the 20 responses listed below can be unpredictable; however, scientific findings and biological common sense both indicate that they 'amplify' in a manner that renders indiscriminate killing ineffective and results in a multitude of detrimental effects on individuals, species populations, and the entire predator-prey ecosystem.

Demographic Compensation: (This is a particularly strong response for coyote populations because the primary reason they kill ungulate neonates, both domestic and wild, is to feed fast-growing pups.)

● Breeding adults produce more pups when there is direct reduction in territorial pack size. There is a weak to negligible effect on litter size at birth; however, the compensatory response of litter survival is remarkable. For example, prior to wolf restoration, adult coyote mortality averaged only 9%, pack size was 6, and litter survival was 28%. After wolf restoration, adult coyote mortality increased to 30% to 50%, pack size fell to 3, and coyote pup survival abruptly rose to 78%—a nearly three-fold increase. Analysis from 20+ field studies indicated a similar response to human exploitation.

● Immigration of breeding adults into the exploited area to fill vacant territories and find available mates. This response can be immediate. I have documented successful coyote litters in territories where the pregnant female was killed one month earlier (ascension by a pregnant beta female—Wildlife Service's own research documents this phenomenon—nearly all non-alpha females are pregnant on an annual basis).

● A higher percentage of females breed and produce pups. Two litters per territory can also occur with abundant/available prey.

● The average age of reproductive females is lowered, eliminating older, less productive alpha females. First-time breeders (young alphas) have higher pup survival than older breeding pairs.

● Increased natal philopatry—yearlings and young betas tend to forego dispersal and continue to reside in the exploited area.

● Regardless of the level of exploitation, the number of breeding pairs in a target area is consistent from year to year unless 70% or more of the coyote population is removed annually. This level of control is extremely difficult and costly to achieve let alone document.

Behavioral Responses:

● Lower pack size results in selection of larger prey items (e.g., ungulate neonates) over more numerous small prey items (e.g., rodents). This is particularly detrimental to livestock when alternate prey abundance is low which is often due to overgrazing practices.

● Adjust vocal communications—less vocal around humans.

● Activity cycles—more nocturnal and less diurnal.

● Denning behavior (guarding and location)—less susceptible to enemies.

● Avoidance of novel stimuli including control techniques. Perceived avoidance of sustained control activities.

Changes in the Culture/Society:

● Increases in information sharing within and between new territorial pack members; this leads to increased exposure to novel prey (livestock).

● Because there is a strong shift to fewer subordinates—betas are immediately recruited to alpha breeding status—livestock-killing alpha adults are predominant in the population structure.

● Killing the alpha male results in immediate replacement or the remaining pack breaks apart and disperses to form breeding pairs elsewhere.

● Indiscriminate control methods have accelerated and amplified selection pressures to perpetuate a 'dispersal genotype' adapted to rapidly colonize and successfully reproduce.

Remember that during the predator eradication era (approximately 1860's to 1960's), large carnivore populations declined substantially (with regional extirpation) while coyotes tripled their abundance and distribution across North America.
● Their cultural evolution likely interacts with their biological evolution to further accelerate and amplify selection pressures.

Ecological Impacts:
● Mesopredator release: Decrease in apex predator populations reduces the competition and/or intraspecific killing rates with other predators or mesopredators (e.g., foxes, raccoons, skunks, feral cats, etc.). This causes an increase in their abundance (i.e., release), which in turn, can have detrimental effects on other species (e.g., ground-nesters, songbirds, amphibians, and rodents) and other unintended 'ripple' effects or trophic cascades.
● Loss of ecosystem services: alleviation of control pressures on prey populations (e.g., rodents, large herbivores) can lead to vegetation changes.
● Loss of ecosystem services: Disruption and increase of disease spread.
● Loss of subsidies to scavengers (e.g., wolves, coyotes provide food for many other species).

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