Wildlife Contraception

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Abstract

Wildlife contraception prevents wild animals– mostly mammals, although sometimes birds– from having offspring. In addition to preventing human-wildlife conflict and ecological damage with less suffering than lethal control does, wildlife contraception may improve survival and increase longevity. Several forms of contraception, including hormonal contraception, surgical sterilization, and immunocontraception, have been developed. Expanding research into contraception may be one of the most effective ways to help wild mammals and perhaps birds.

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Why Use Contraception On Animals?

There are two primary uses of wildlife contraception to promote wild-animal welfare.

First, people may wish to limit populations for some reason, and contraception may be the most welfare-promoting means of achieving that goal. Most obviously, wildlife contraception is used in zoos and aquariums to manage breeding programs and prevent the existence of animals who cannot be adequately cared for (Asa & Porton, 2005, pp. xv–xvi). Invasive species are a serious threat to ecosystem preservation and may also cause harm to humans (ibid: xiv-xv). Contraception permits control of wildlife populations in national parks and other areas that do not permit hunting, trapping, or poisoning (ibid: 195). In urban areas, hunting is generally not legal, wise, safe, or acceptable to the public (ibid: 195). Some species are protected from hunting by law (ibid: 195).

Overabundant wildlife populations may result in ecosystem degradation, destruction of food crops and even injury and death to humans (Asa & Porton, 2005, pp. xiii–xiv). (Jewell, 1982) argues that there are four kinds of overabundance, or animal populations being higher than they 'should' be. First, the population may be so high that it interferes with human goals, such as by spreading diseases or killing livestock (ibid: 7-8). Second, the population may be so high that it reduces the population of more favored species, such as charismatic herbivores or particular trees (ibid: 8). Third, the population may be over the carrying capacity, perhaps because of human intervention (ibid: 9).

Hunting, trapping, poisoning, or introducing diseases or predators all typically cause suffering (see for example (Sharp & Saunders, 2011)). Wildlife contraception may allow the populations to be controlled without causing undue suffering to animals.

The fourth form of overabundance is worth discussing in greater detail. When populations are high enough, the welfare of the animals tend to decrease (Jewell, 1982, pp. 8–9). In particular, populations below the carrying capacity tend to have higher welfare than populations at the carrying capacity (ibid: 8-9). Populations kept below the carrying capacity by hunting tend to be larger, fatter, and healthier (ibid: 8). High populations tend to have poor body condition, high parasite burdens, and high infectious disease prevalence (Gary Killian, Diehl, Miller, Rhyan, & Thain, 2006, p. 84). For example, deer populations below the carrying capacity tend to have high body weights and nutritional status and low abomasal parasite counts (Coulson, 1999, p. 165). Although the fourth form of overabundance is correlated with the third form, they're separate: a population may have decreased welfare due to its high population but still be below the carrying capacity.

In general, higher animal densities tend to increase contact rates and thus increase the spread of disease (Gary Killian et al., 2006). Diseases linked to high animal populations include tick-borne encephalitis in ungulates, classical swine fever in wild boar, bovine tuberculosis in ungulates, avian tuberculosis in the red-legged partridge, and sarcoptic mange in Spanish ibex and Barbary sheep (ibid: 83). Many species, such as lagomorphs like rabbits and hares, are understudied, but it may safely be assumed that high densities also increase disease transmission in those species (ibid: 82).

One tractable strategy for reducing wild-animal suffering may be to maintain populations below the natural carrying capacity.

Introduction to Wildlife Contraception

Minimizing the pain and distress to wild animals while controlling populations is a complicated topic (Asa & Porton, 2005, pp. 6–7). Some forms of contraception, such as surgical sterilization, may lead to pain, disability, or death (ibid: 6). Reversible contraception is still experimental and long-term studies on safety, toxicity, and carcinogenesis have not been performed (ibid: 9). Contraception may change social behaviors in ways that are beneficial, negative, or neutral (ibid: 6). It is likely that the effects of psychosocial changes on welfare are species-specific (ibid: 6-7). Failed attempts at contraception may cause unnecessary distress to animals (ibid: 7). Since fertility control is often very expensive, it may take resources away from other, more cost-effective ways to improve animal welfare (ibid: 7).

For every study that finds a collateral effect of wildlife contraception, there is another study of a different species or fertility control method that finds no such effect (Ransom, Powers, Thompson Hobbs, & Baker, 2014, p. 262). To understand the use of fertility control on a species, we must think about "species biology, reproductive system, physiology, behavioral ecology, population biology and ecological context" (ibid: 262).

With rare exceptions, wildlife contraception has generally only been studied in medium to large mammals (Jay F. Kirkpatrick, Lyda, & Frank, 2011, p. 40). Studies are particularly likely to concentrate on the orders Perissodactyla (especially horses), Artiodactyla (especially deer and domestic cows), and Carnivora (especially felids) (Gray & Cameron, 2010, p. 46). Data is generally sparse in mammals other than carnivores, ungulates, and primates (Asa & Porton, 2005, p. 177). Most studies are relatively short-term and only address health concerns, without considering the effects of contraception on the animal's affective states, experience of the environment, nutrition and ability to perform natural behaviors (Hampton, 2017, pp. 176–177).

Much of the research on wildlife contraceptives is confined to captive populations (Asa & Porton, 2005, p. 214). While there is a need for more and better wildlife contraceptives, perhaps the greatest need is for more effective delivery methods and more qualified people to apply contraceptives in the field (ibid: 214-215).

History of Wildlife Contraception

The study of wildlife contraception dates back to the 1950s (Jay F. Kirkpatrick et al., 2011, p. 40). While early attempts were pharmacologically successful, they generally failed practically for reasons such as passage through the food chain, regulatory issues, high cost, difficulty with remote delivery, toxicity, social and behavioral changes that were potentially harmful to animal welfare, and health risks in pregnant animals (ibid: 40-41). Before the 1980s, there were few published attempts to use contraception on wild animals, and few of those attempts were successful (Asa & Porton, 2005, p. 196). Even seemingly promising contraceptives have been derailed by lack of bait acceptance, problems with absorption, the impracticality of implants, or the necessity of treating the wildlife daily (ibid: 196-197).

The development of immunocontraceptive vaccines led to significant progress in free-ranging wildlife contraception (Jay F. Kirkpatrick et al., 2011, p. 41). In 1994, there was the first management-level application of contraceptives to free-ranging wildlife (Asa & Porton, 2005, p. 202). The PZP vaccine was used on a 166-animal herd of wild horses on Assateague Island National Seashore (ibid: 203). Within a year, zero population growth was attained and maintained for over a decade, at a cost of $1500 a year plus the cost of labor (ibid: 203). Body condition increased, mare and foal mortality decreased, and maximum lifespans increased by nearly a decade (ibid: 203). The PZP vaccine was found to be reversible for up to five years of consecutive treatment; it is unknown whether longer periods of treatment are also reversible (ibid: 203).

Nevertheless, there remain many difficulties in using wildlife contraception, including identifying successful contraceptive agents, documenting safety, developing methods for delivery, and actually altering populations (Jay F. Kirkpatrick et al., 2011, p. 41). Few inventions of new wildlife contraceptives were made with an eye to the physiological and logistical difficulties of contracepting free-ranging wildlife populations (Asa & Porton, 2005, p. 198). By 2012, management attempts to control free-ranging populations with contraception barely numbered in the double digits, including six wild horse populations, three white-tailed deer populations, and two African elephant populations (Rutberg, 2013, p. S38). Today, fertility management is still not a tool in most wildlife managers' arsenal (Jewgenow, 2017, p. 268).

The Ideal Wildlife Contraceptive

Ideal criteria for a wildlife contraceptive includes (Giovanna Massei & Cowan, 2014, p. 3):

1. No or acceptable side effects on wildlife physiology, behavior, and welfare;
2. Effective when administered in a single dose;
3. Render all or the majority of animals infertile for the rest of their lives
4. Ideally prevents reproduction in both sexes, but only inhibiting contraception in females would also work;
5. Does not interfere with pre-existing pregnancy or lactation (this may compromise welfare);
6. Inexpensive;
7. Remote-deliverable (to reduce the costs of administering the contraceptive);
8. Does not enter the food chain;
9. Species-specific; and
10. Stable under a wide range of field conditions.

A similar list, about wild horse contraception, lists (Turner & Rutberg, 2013, p. S103):

1. Highly effective;
2. Multiyear duration;
3. Reversible;
4. Intact social structure and sexual behavior;
5. No effect on existing pregnancy;
6. No toxicity to recipient or applicator;
7. Remote-deliverable;

8. Cost-effective; and
9. Does not enter the food chain.

Unfortunately, no currently available fertility control agent has all of those desirable characteristics (Giovanna Massei & Cowan, 2014, p. 3).

Some of these traits are less important for certain species than they are for others. Safety in pregnant animals is less important in species that spend less of their time pregnant (Asa & Porton, 2005, p. 198). Social effects are less important in species with less complex social organization (ibid: 198).

(Turner & Rutberg, 2013, p. S103) says that the contraceptive should be reversible, while (Giovanna Massei & Cowan, 2014, p. 3) says a contraceptive should ideally render an animal infertile for their entire lives. Again, this depends on the species discussed. For example, reversibility is less important in overabundant species in national parks and in species that cause significant human-wildlife conflict (Asa & Porton, 2005, p. 198).

Many people may approve of a contraceptive that also causes abortions, since it is more efficient: instead of preventing pregnancies, it both prevents pregnancies and ends them. However, many people consider fetuses to have moral worth. Even people who do not themselves consider animal fetuses to be moral patients may prefer a contraceptive that does not cause abortions, since it may increase public acceptability.

While species specificity is desirable for humane control of species that cause human-wildlife conflict, such as deer and rats, it may or may not be desirable from a wild-animal suffering perspective. On one hand, a non-species-specific contraceptive may maintain an entire ecosystem below the carrying capacity, making it far more cost-effective than species-specific contraceptives for each species. On the other hand, without some method of limiting the spread of the contraceptive, it could easily be primarily consumed by a species one does not want to maintain below the carrying capacity (e.g. an endangered species, a species with unusually high welfare, an economically important species, a keystone species that benefits many other species). Since no contraceptive is equally effective in every species, the use of contraceptives throughout an ecosystem may cause serious changes in relative species abundances, and thus species interactions and ecosystem functioning.

Criterion	**Sterilization**	**Hormonal contraception**	**PZP vaccines**	**GnRH vaccines**	**ContraPest**
Effective	Yes	Sometimes	Yes	Yes	Yes
Reversible	No	Yes	Yes	Yes	No
Duration	Forever	Days to years	Years	Years	Forever
Intact behavior	No	Varies	Somewhat	No	No
Effect on pregnancy/lactation	Varies	No	No	No	No?
Toxicity	No	No	No	No	No
Remote-deliverable	No	No	Yes	Yes	Yes
Cost-effective	No	No	Varies	Varies	Varies
Enters food chain	No	Yes	No	No	No
Works on both sexes	Yes	Yes	No	Yes	Yes
Species-specific	N/A	No	No	No	Somewhat
Field-stable	N/A	Somewhat	Yes	Yes	Yes

Contraception In General

Effectiveness and Reversibility

Effectiveness

Assessing a contraceptive's effectiveness and reversibility may seem simple: no offspring should be born while the contraceptive is in use, and offspring should be born once the contraceptive is no longer being used (Asa & Porton, 2005, p. 53). However, as in all biological systems, many factors complicate a seemingly straightforward assessment (ibid: 53). To consider whether a contraceptive is effective, we must consider whether the female was pregnant before the contraceptive started, how long the contraceptive takes to work, whether the contraceptive was used as intended (e.g. the bait was eaten, the injection was delivered, or the intrauterine device or implant stays in place), and how accurately the duration of efficacy can be assessed (ibid: 53-55). Duration of efficacy of implants, injectable depots, and vaccines varies substantially based on individual factors and must always be given as a range (ibid: 58).

In free-ranging populations, a contraceptive is generally considered effective if 50 to 60% of treated animals are sterile, because managers are trying to control the reproductive rate in general, not whether any individual animal reproduces (Asa & Porton, 2005, p. 84).

Some species experience residual infertility even after the contraceptive usually stops working (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 261), which makes the contraceptive more effective than it would naively seem.

Some taxa, such as pinnipeds and cetaceans, are not typically contracepted in captivity, which means there is a dearth of data on contraceptive effectiveness and reversibility in these species (Asa & Porton, 2005, p. 168).

Up-to-date information on which contraception is most appropriate for which taxa, intended for use by zoos, can be found here (https://www.stlzoo.org/animals/scienceresearch/reproductivemanagementcenter/aza-contraception-program/) ("AZA Contraception Program :: Saint Louis Zoo," n.d.).

Population Size Reduction

The effectiveness of a contraceptive in controlling population size varies over time (Turner & Rutberg, 201 (https://paperpile.com/c/uGNMHI/OUytN/?locator=S105)3, p. S105) (https://paperpile.com/c/uGNMHI/OUytN/?locator=S105). For example, mortality rates may be higher some years due to extreme weather conditions, hunting, disease, collisions with vehicles, or increased predation (ibid: S105). If mortality rates are higher, contraceptives will appear more effective. Emigration and immigration may also increase or decrease the apparent effectiveness of a contraceptive in controlling populations, and may vary over time due to changing conditions in other sites (ibid: S105-S106). Factors such as responsiveness to treatment, access to animals, and the field viability of the contraceptive may also change over time (ibid: S107).

Fertility control tends to be rather slow in reducing population size, although it is useful for maintaining populations at a desired size (Giovanna Massei & Cowan, 2014, p. 11; Giovanna Massei, Roy, & Bunting, 2011, p. 88).

Initial models argued that small species with high fertility and low survival would be the easiest to manage with contraceptives, because for these species fecundity is a more important density-dependent factor than survival (Giovanna Massei & Cowan, 2014, pp. 11–12). More advanced models suggest that long-lived species are easier to control, because less of the population needs to be treated and lifelong contraceptives last longer (ibid: 12). Duration is more important for species in the latter category; even a single-year treatment may reduce populations for species with high recruitment rates (Cowan & Massei, 2008, p. 225).

Contraception tends to work poorly to control open populations of promiscuous breeders and well to control small, closed populations (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 262). In a closed population, there is no immigration, while in an open population there is immigration. Let us consider a long-lived, low-fecundity species. More than half of females must be treated in closed populations to achieve moderate reduction in growth (ibid: 262-263). However, more than 90% of females must be treated in open populations, where immigration can compensate for lower birth (ibid: 263). A promiscuously breeding species is one in which males mate with many females and females mate with many males, so any animals to whom contraception is not applied may easily find similarly fertile partners. In highly promiscuous breeders, achieving population goals through contraception may not be feasible (ibid: 263).

Some models suggest that contraception will be most effective to control species with high reproductive and low survival rates, such as rats and some birds (Fagerstone, Miller, Killian, & Yoder, 2010, pp. 21–22). In particular, these models find contraception may be very effective in populations where the age at first reproduction is under three (ibid: 21). The high birth rates of those populations may mean that reducing birth rates reduces populations more sharply. However, since short-lived, high-fecundity populations have high recruitment rates, the fertility treatments must be applied frequently (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 263), which makes fertility control more expensive and less effective.

For some species, contraception may be more effective than initial studies suggest. Males of some species prefer contracepted females to uncontracepted females (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 261). Conversely, in other species contraception may lead to a compensatory reproductive response, which reduces the effect of contraception (ibid: 261). If the compensatory reproductive response occurs after birth (e.g. increased juvenile survival), contraception may not reduce population sizes (Tuyttens & Macdonald, 1998a, p. 353), although of course the effects may be welcome for welfare reasons. Conversely, if density-dependent regulation occurs before the part of the reproductive cycle interfered with by contraception (e.g. female-female competition), the compensatory reproductive response may have little effect (ibid 353).

Compensatory density-dependent processes tend to be more effective at raising populations after culling than after contraceptive use, particularly in species where fecundity plays a larger role than survival in population growth (Giovanna Massei & Cowan, 2014, p. 11). Potential compensatory effects include increased juvenile survival due to decreased competition, increased birth rates in fertile individuals due to greater resource availability, and increased immigration or decreased dispersal (Asa & Porton, 2005, p. 91). If a contraceptive alters behavior, dominant individuals may lose their dominance and be replaced by fertile individuals (ibid: 91). Similarly, if a contraceptive reduces the drive to maintain a territory, the contracepted animal may be replaced by a fertile animal who did not previously have a territory (ibid: 91). In theory, in certain special circumstances, contraception may increase population, such as if the sterilization of a dominant female causes all her subordinates, previously unable to breed, to be able to breed (Caughley, Pech, & Grice, 1992). However, infertile animals remain in the population, which may prevent some forms of compensation (Cowan & Massei, 2008, p. 220).

Fertility control may affect immigration and emigration in a population (Giovanna Massei, Dave Cowan, Douglas Eckery, USDA APHIS National Wildlife Research Center, & Authors, 2014, p. 221). If fertility control reduces population density, more animals may immigrate into the area (ibid: 221). Conversely, males may emigrate from the area in search of fertile females (ibid: 221). For example, brushtail possums tend to immigrate into areas with high percentages of sterilized possums, so surgical sterilization does not actually reduce local possum populations (D. Ramsey, 2005). Presumably, however, contraception still reduces overall possum populations.

Reversibility

Time to reversal of a contraceptive may also be difficult to assess (Asa & Porton, 2005, p. 59). Non-contraceptive factors that influence birth rate include reproductive history, age, body weight, health, season, social status, fertility of the partner, and genetic compatibility of the couple (ibid: 59). Reversibility studies should always have a control group, preferably of animals matched in age and number of previous young (ibid: 59). Potential ways of measuring time to reversal include latency to clearance of the contraceptive, resumption of ovarian cycles, first conception, and first birth of live young (ibid: 59-61). For males, the best metric is latency to spermatogenesis (ibid: 62-63).

Physical Health Effects

Most contraceptives have only been adequately tested for safety in humans and laboratory animals, mostly rats, mice, primates, and dogs (Asa & Porton, 2005, p. 66). Safety for other wildlife has been inferred from those studies, but the inference may be inaccurate, as reproductive function and structure often vary among mammalian species, especially in females (ibid: 66). It is not practical to test contraceptives for safety in every species that might need a contraceptive, because clinical trials are expensive and in many cases it may be impossible to obtain a sufficient sample of captive animals from a particular species (ibid: 66-67).

In nonhuman animals, many side effects are common as a result of contraceptive treatment (Gray & Cameron, 2010, p. 47). However, most studies find little or no effect on internal organs other than the ovaries or testes (ibid: 48).

Body Condition

Theoretically, it is expected that contraception should improve female body condition, since contracepted females do not gestate or lactate (Gray & Cameron, 2010, p. 48). However, while some studies find an improvement in body condition, most find no effect (ibid: 48). In some cases, contraception may worsen body condition. For instance, some species spend less time feeding and resting when contracepted, which makes their body condition worse (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 261). Contracepted female elk have lower body fat percentages, perhaps because infertility lowers their exposure to anabolic hormones (ibid: 261). Some deer treated with hormonal contraception had worse body condition and a few stopped eating entirely (ibid: 261).

Reproductive System Effects

In one review, most studies found changes in ovarian structure and function, which is not surprising because contraceptives act directly on the reproductive system (Gray & Cameron, 2010, p. 47).

Injection Site Reactions

Several studies found that injectable contraception resulted in inflammation at the injection site (Gray & Cameron, 2010, p. 48). Inflammation rates can be reduced by using a different adjuvant, and injection-related inflammation usually heals quickly with no long-term side effects (ibid: 48).

Disease Transmission

There are many theoretical reasons one would expect an effect of wildlife contraception on disease transmission (Gray & Cameron, 2010, p. 50; G. Killian, Fagerstone, Kreeger, Miller, & Rhyan, 2007, p. 268). If animal populations fall below a threshold density, the disease will no longer be maintained in the population (G. Killian et al., 2007, p. 268). Fertility control is slower than other population-reduction methods, like culling, which implies it will take longer to have effect (ibid: 268).

Suppressing reproductive behavior eliminates contact associated with courtship, estrous, or intramale competition, thus reducing the risk of disease transmission (G. Killian et al., 2007, p. 268). Fertility control eliminates the risk of vertical (mother-to-child) transmission (ibid: 268). Suppressing reproductive behavior also prevents venereal disease and diseases related to pregnancy (G. Killian et al., 2007, p. 268; Miller, Fagerstone, & Eckery, 2013, pp. S90–S91). For example, contraception may be an effective method of reducing brucellosis in bison, because brucellosis is primarily transmitted through contact with miscarried fetuses or calving, which can be prevented by preventing pregnancy (Miller, Rhyan, & Drew, 2004). Conversely, if contraception leads to an increase in sexual interactions, disease transmission rates may increase (Gray & Cameron, 2010, p. 50). For this reason, preventing ovulation is preferred to preventing fertilization when the goal is to control disease (Giovanna Massei & Cowan, 2014, p. 12).

Most studies find no effect on disease transmission rate (Gray & Cameron, 2010, p. 50). In at least one species contraception increased disease transmission rate (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 261).

Survival

While few studies have examined contraception use in the wild for a long enough period to notice the effects on survival and longevity, three-quarters of studies that did examine it found an increase in survival or longevity (Gray & Cameron, 2010, p. 50). Contraception is particularly likely to improve survival among females (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 261). In ungulates, contraception often improves both survival and health condition (Giovanna Massei et al., 2014, p. 221). Wildlife contraception may increase survival by causing animals to spend fewer resources on reproduction and by reducing the level of competition faced by the offspring of fertile animals (Gray & Cameron, 2010, p. 50). This suggests that use of wildlife contraception will not necessarily have a negative effect on abundance which increases the species's risk of extinction.

From a theoretical perspective, it is possible that contraception that prevents fertilization would decrease longevity in males (Asa & Porton, 2005, p. 92). If females have repeated estrus cycles, males may spend more energy competing for and mating with females at the expense of resting and foraging (ibid: 92). Thus, males may have lower survival, particularly over winter (ibid: 92). The males may also experience more aggression and fighting, which could lead to injury and potentially death (ibid: 92).

Psychological Effects

All forms of contraception cause some suffering or remove the opportunity for some positive experiences (Hampton, 2017, p. 184). If nothing else, contraception always deprives an animal of the opportunity to parent (ibid: 184). Significant, long-term changes in physiology may affect an animal's ability to perform natural behaviors or cope with problems in their environment (ibid: 171). However, it is possible that the advantages of a contraceptive outweigh the negative effects. Forms of contraception that preserve the animal's normal hormonal balance may allow for more normal behavior than endocrine-suppressing contraception does, and thus lead to overall better well-being (ibid: 184).

While most studies found changes in physiology and behavior, these effects may be too small to have any effect on animal welfare (Gray & Cameron, 2010, p. 49). However, few studies directly assess wild animal welfare, such as by studying chronic stress indicators (ibid: 49). Studies rarely consider the welfare of untreated animals such as males, even though contraceptives may also change their behavior (ibid: 49-50). Many studies were performed on captive animals, which may not generalize to free-ranging wildlife (ibid: 50).

Activity Budgets

Most studies suggest that activity budgets remain unchanged (Gray & Cameron, 2010, p. 48).

Social Structure

Studies of social behavior show mixed results (Gray & Cameron, 2010, p. 49). Contraception may decrease fidelity to family groups (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 261). Depending on the species, contraception may increase, decrease, or leave unchanged time spent with conspecifics or potential mates (ibid: 261). Most studies of the effects of contraception on social interactions use opportunistic observations or are of short duration, meaning that the results have limited generalizability (Gray & Cameron, 2010, p. 49).

Although few studies have been conducted, from a theoretical perspective it is possible that the absence of young has a negative effect on the welfare of individual females and the social group as a whole, since the animals are not able to engage in natural parenting behavior (Asa & Porton, 2005, p. 90). In zoo animals, the absence of parenting behavior is thought to reduce the animal's welfare (Hampton, 2017, p. 174). Parenting is an important and complex natural behavior (ibid: 174). By not permitting animals to parent, we may deprive them of a rewarding experience or an opportunity to satisfy their preferences (ibid: 174).

From a theoretical perspective, infertility may lead to the destruction of pair bonds, but in studies of canids pair bonds seem to be maintained (Asa & Porton, 2005, p. 90).

Most studies find minimal impact on home range size and movement patterns (Gray & Cameron, 2010, p. 49).

The impact of contraception on primate behavior is understudied and may be very complex, given their complex sociosexual behavior (Asa & Porton, 2005, pp. 144–145).

Elephant contraception has a variety of possible effects on elephant social structure. If elephant females have fewer calves, it may reduce family group cohesion, leading to larger herds and altered social structures (Kerley & Shrader, 2007, p. 182). Elephants learn how to raise calves through allomothering (ibid: 182). Contraception may reduce allomothering opportunities, thus causing higher mortality rates among elephants' first calves (ibid: 182). In addition, with fewer calves and larger herds, calves may be harassed by large numbers of potential allomothers (ibid: 182). This may increase stress and reduce milk production in their mothers (ibid: 182). Inability to reproduce may lead to depression and attempted calf kidnapping (ibid: 182).

Aggression

Depending on the species, contraception may increase aggression, decrease it, or leave the amount of aggression unchanged (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 261).

Using contraception on males may reduce aggression (Asa & Porton, 2005, p. 190). However, the effects of contraception on aggression are poorly understood (ibid: 191). The effects differ based on season, age, species, demography, dose and duration of treatment (ibid: 190). Aggressive behavior is complex and dependent on external factors, such as competition (ibid: 190). Males may express learned aggressive behavior even with a below-average level of testosterone (ibid: 190). Certain aggression-related receptors or pathways may be primed by high perinatal testosterone concentrations in males (ibid: 190).

In elephants, contraception may cause increased aggression (Kerley & Shrader, 2007, p. 181). Female elephants usually come into estrus once every four years, but when using contraception they come into estrus four times a year (ibid: 181). Male elephants chase and mount females, who are usually smaller, and may cause injury (ibid: 181). Male elephants may also fight each other over mating opportunities, perhaps resulting in elephant deaths during fights (ibid: 181).

Reproductive Effects

The majority of studies showed changes in estrus and breeding behavior (Gray & Cameron, 2010, p. 49). Paradoxically, in hierarchically structured species where females suppress subordinates' breeding, if sterile dominant females lose their status productivity may increase overall (Giovanna Massei & Cowan, 2014, p. 12). (Of course, if they retain their status, contraception will decrease productivity as usual (ibid: 12).)

In most cases, not enough research has been performed to come to conclusive answers about the effects of contraception on post-reversal stillbirth rates, litter size, or infant survival (Asa & Porton, 2005, p. 62). Effects on pregnancy and lactation will be discussed in the appropriate section.

Ecological and Evolutionary Effects

90% of studies of wildlife fertility control focus on individual-level effects (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 262). Only 6.5% consider behavioral or indirect demographic effects on population-level assessment of fertility control, and only about three percent quantitatively model these effects (ibid: 262).

Fertility control may have complex genetic effects (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 263). Managers may purposely or accidentally select animals with particular traits for contraception, reducing the presence of that trait in the population (ibid: 263). Contraception may also favor animals who make certain behavioral decisions, such as reproducing with fertile females or increasing or decreasing aggression (ibid: 263-265). If dominant males are targeted for sterilization, most offspring will be fathered by males who would not have been the primary breeders or who females do not prefer, potentially causing severe genetic consequences (Asa & Porton, 2005, p. 91).

If only certain females breed, there may be a risk of inbreeding in future generations (Jewgenow, 2017, p. 273).

When one prey species becomes less abundant due to contraception, predators may switch to predating on a different prey species (Jewgenow, 2017, p. 273). The effects of this are unknown.

Practical Issues

Wildlife contraception faces many practical issues. There may be regulatory concerns, because free-ranging wildlife may be food for nonhuman scavengers and predators, as well as for humans (Asa & Porton, 2005, p. 196). Public opinion about whether the animal is beautiful or vermin may affect which contraceptives are socially acceptable (ibid: 196). There are innate difficulties in contracepting wild animals which are wary of humans and may resist contraceptive application (ibid: 196). Political opposition, economic issues, and cultural taboos may make contraception nonviable (ibid: 199).

Cost-Effectiveness

Contraception is very expensive. Depending on other factors, the cost to render a single animal infertile ranges from $25 to $1000 (Giovanna Massei & Cowan, 2014, p. 13). Costs are affected by animal density, the level of training of the people capturing animals and providing contraceptives, approachability of animal, land access, and efficacy of the treatment (ibid: 13). Wildlife contraception is particularly cost-ineffective for states compared to lethal control, which actually earns states money through sales of licenses to hunters (Fagerstone, Miller, Killian, et al., 2010, p. 22). However, wildlife contraception may be cost-effective compared to other forms of non-lethal control or if the state has to pay people to cull the animals (J. F. Kirkpatrick, 2007, pp. 550–551). It is always important to consider the counterfactual when assessing the humaneness and cost-effectiveness of contraception (ibid). (It's important to distinguish cost-effectiveness from a cost-benefit analysis: cost-effectiveness considers only how much contraception costs to reduce populations to a certain level, while a cost-benefit analysis considers other positive side effects of contraception.)

Regulatory Issues

Wildlife contraception faces regulatory issues. The regulation around testing and application of contraception to animals is complex because of “issues such as ownership of animals, legal authority for managing the animals, classification of some species… as food animals, and the often confusing management authority between state and federal entities” (Asa & Porton, 2005, pp. 21–22). County, municipality, and park regulations must be considered and often derail attempts at wildlife contraceptive use (ibid: 22). For example, resistance from state fish and game industries and the FDA policy of only treating ear-tagged animals long prevented the use of immunocontraceptive vaccines on urban deer in the United States (ibid: 207). Public opinion has tremendous influence on whether wildlife contraceptives are used, even though it is often deeply misinformed (ibid: 24). Data requirements, registration timelines, and costs have been increasing, which is stifling innovation (Humphrys & Lapidge, 2008, p. 583). At times, millions of dollars can be invested into research without a registered product to show for it (ibid: 583).

As of 2010, only the United States had registered wildlife contraceptives (that is, permitted them to be used for purposes other than research) (Fagerstone, Miller, Killian, et al., 2010, p. 20). Wildlife contraceptives are currently regulated by the EPA, although in the past they were regulated by the FDA (ibid: 20). To register a product, a company must submit a series of studies on product chemistry, toxicity, efficacy, harms to non-target species and environmental fate (ibid: 20). Registering a GnRH vaccine cost between $200,000 and $500,000 (National Research Council, Division on Earth and Life Studies, Board on Agriculture and Natural Resources, & Committee to Review the Bureau of Land Management Wild Horse and Burro Management Program, 2013, p. 130). In general, injectable contraceptives are easier to register than oral contraceptives, because they pose less risk of harm to air, water, soil, or nontarget species (Fagerstone, Miller, Killian, et al., 2010, p. 20). The registration process sometimes takes several years (ibid: 20). Currently approved wildlife contraceptives may only be used by certified pesticide applicators, because of worries about animal welfare, hazards to the applicators, and inappropriate use or use in nontarget species (ibid: 20). This likely makes contraceptives more expensive to use.

Seventeen American states have specifically banned administering fertility control without a permit from the state wildlife department (Eisemann, O’Hare, & Fagerstone, 2013, p. S50). Many others ban fertility control without a permit without a specific law allowing them to do so: for example, the wildlife department might classify fertility control as an illegal means of take (a nonpermitted kind of hunting or trapping) or consider banning fertility control to be one of the things they have the discretion to do as the agency that handles wildlife (ibid: S50). In all states, research on contraceptives in free-ranging wildlife is legal with the permission of the wildlife department (ibid: S50). Some states, under public pressure to expand the use of fertility control, have begun to create a permitting process for this research, which often requires an explanation for why hunting and other traditional management processes aren’t appropriate (ibid: S50). While this paper is from 2013, I contacted one of the authors and she says it continues to be an accurate description of the state of wildlife contraception regulation (O’Hare, 2018).

The regulation in the European Union is at least as complicated as the regulation in the United States (Rutberg, 2013, p. S39). In the EU, potential contraceptives must be approved both by the EU and by the individual member country that one wishes to use the contraceptive in (Humphrys & Lapidge, 2008, pp. 582–583). Further, contraceptives intended for use on larger mammals are likely to be considered veterinary medicines, which require approval from additional agencies in both the EU and the member country (ibid: 582-583).

In New Zealand and Australia, contraceptive approval appears to be rather simpler, only requiring the approval of the Environmental Risk Management Agency/Food Safety Agency or the Australian Pesticides and Veterinary Medicines Authority, respectively (Humphrys & Lapidge, 2008, p. 58).

Public Opinion

Wildlife contraceptive use may be unpopular in some circles (Fagerstone, Miller, Killian, et al., 2010, p. 24). However, suburban residents who experience human-wildlife conflict may disapprove of lethal control and prefer fertility control, particularly if hunting and trapping are illegal in the area (ibid: 24). Non-lethal animal control in general and fertility control in specific are becoming more popular, particularly among urban and suburban residents, while lethal control is becoming increasingly unpopular (ibid: 24). Fertility control may be particularly popular when human-wildlife conflicts are caused by mating activity, such as burrowing and nest construction (Cowan & Massei, 2008, p. 220).

Proponents of wildlife contraception include (J. F. Kirkpatrick, 2007, p. 548):

- scientists who are intellectually interested in wildlife contraceptives;
- wildlife managers who wish to expand their options;
- animal welfare advocates who prefer non-lethal control;
- habitat managers and public health officials who wish to control the environmental and health effects of wild animal overpopulation;
- zoo managers who face unlimited population growth and limited space; and
- politicians who believe the public supports wildlife contraception.

Many people, particularly animal rights advocates, have ethical objections to lethal control of wild animals, which means an effective method of nonlethal control is likely to be far more popular (Asa & Porton, 2005, pp. xii–xv). Many people, including the author of this document, believe that contraception is ethical when it prevents suffering of a sentient being (ibid: 5).

Fertility control supporters often believe that animals have a right to life and either should not be killed or should only be killed as a last resort (Bruce Lauber, Knuth, Tantillo, & Curtis, 2007, p. 126). Fertility control supporters typically prioritize the animal's quality of life, although they may be willing to preserve an animal's life even if the animal is suffering (ibid: 126-127). Fertility control supporters prioritize individual animals over ecosystems (ibid: 127-128). Fertility control supporters care about humaneness, protecting other wildlife and pets, political acceptability, and avoiding violence (Fagerstone, 2002, p. 5). They also tend to believe contraception is effective (ibid: 5). Proponents of wildlife contraception care about the suffering of deer and prefer that herd sizes be set by nature alone (Kreeger, 1997, p. 252). (It is unclear from the research whether proponents understand that wildlife contraception is also a form of human intervention into nature.)

Opponents of wildlife contraception include (J. F. Kirkpatrick, 2007, p. 548):

- hunters who believe it may replace hunting as a means of population control;
- state wildlife agencies who are aligned with and rely economically on hunters; and
- some animal welfare organizations for various reasons.

Some animal rights advocates argue that contraception is unethical because it is interfering with the animal's control over its own reproductive life (Asa & Porton, 2005, pp. 4–5). Some people argue that hunting is the only ethical method of population control, because hunting is a natural biological process which controls excess populations and because it connects humans to nature (ibid: 5).

Fertility control opponents support killing animals as a solution for human-wildlife conflict even if other options are available (Bruce Lauber et al., 2007, p. 126). Fertility control opponents often believe that contraceptives reduce the animal's quality of life or that highly abundant animals have low quality of life to begin with (ibid: 127). Fertility control opponents typically prioritize biodiversity and the balance of nature over the welfare of the individual animal (ibid: 127-128). Some fertility control opponents may object to fertility control because it is perceived as getting rid of the animal's 'wildness' or preserving a non-native species that should be eliminated (ibid: 128-129). Opponents of fertility control care about preserving hunting opportunities, low management costs, and quickly reducing population size (Kreeger, 1997, p. 252).

Both supporters and opponents, however, agree that animal control policy should be science-based, involve stakeholders, and be effective (Bruce Lauber et al., 2007, p. 130).

There is a three-step approach to studying wildlife contraception (Asa & Porton, 2005, pp. 198–199):

1. Is a contraceptive capable of inhibiting fertility in a particular species?
2. Can the contraceptive be delivered in the wild?
3. Can a population effect be achieved in the field? That is, can enough of the population be made infertile to cause a contraceptive effect?

The general public generally ignores questions two and three and only pays attention to whether a contraceptive exists when advocating for wildlife contraception (ibid: 199).

Unfortunately, the very popularity of wildlife contraception may make research more difficult. At present, wildlife management is generally considered to be synonymous with hunting (Rutberg, 2013, p. S40). The general public generally supports hunting as a management tool that prevents greater harms such as starvation, but is leery of purely recreational hunting (ibid: S40). Wildlife management agencies have control over scientific research conducted on wildlife (ibid: S40). There have been several cases of wildlife management agencies delaying or denying wildlife contraception research applications or placing so many limitations on them that research is impossible (ibid: S40). They may also spread misinformation to the media (ibid: S40-S41). (It is perhaps not a coincidence that one of the most successful uses of wildlife contraception is on wild horses in America, who are not hunted.)

Research

Providing contraception to nonhuman animals is inherently far more difficult than providing contraception to humans, who can be expected to show up at a clinic and take daily pills (Rutberg, 2013, pp. S39–S40). Wild animals are not likely to make themselves available for repeated treatments (ibid: S40). For this reason, wildlife contraception must be long-acting, which means studies to show its effectiveness take three to five years (ibid: S40).

Free-ranging wildlife contraceptive development is likely to be underfunded (Asa & Porton, 2005, p. 215). Drug companies generally require sales of millions of doses a year for research to be profitable, and few wildlife contraceptives will reach that level of sales (ibid: 215). For that reason, wildlife contraceptives are generally developed by nonprofits or the government, or are developed for use in domestic or companion animals (ibid: 215).

In general, more contraceptive options are available for females than for males (Asa & Porton, 2005, p. 33). Female-directed contraception may be easier because females produce fewer gametes at discrete intervals (ibid: 33). Also, many forms of wildlife contraception are based on human contraception, which tends to be used by females for cultural reasons (ibid: 33).

Surgical Sterilization

In females, removal of the ovaries (ovariectomy) or removal of the ovaries and the uterus (ovariohysterectomy) are common methods of sterilization (Asa & Porton, 2005, p. 33). Females may also be sterilized through tubal ligation or otherwise cutting or blocking the ovarian ducts, but this is understudied in nonhuman animals (Asa & Porton, 2005, p. 33). Techniques for surgical sterilization in deer include laparotomy or laparoscopy with tubal ligation, tubal transection, and ovariohysterectomy (Jason R. Boulanger, Curtis, Cooch, & DeNicola, 2012, p. 276).

Male castration is a simple procedure in most species, although far more difficult in species like elephants, pinnipeds, and cetaceans which have undescended or partially descended testicles (Asa & Porton, 2005, p. 42). If it is desired that males retain their secondary sexual characteristics and male-typical behavior, a vasectomy may be performed on males (ibid: 42). One may also obstruct sperm passage by injecting a sclerosing agent into the vas deferens or cauda epididymis (ibid: 43).

For both males and females, gonadectomy is considered by some scholars to deliver the worst welfare outcomes of any currently available contraceptive (Hampton, 2017, p. 183). Gonadectomy requires capture, anesthesia, and often major abdominal surgery (ibid: 183). It causes irreversible permanent endocrine suppression, which causes permanent changes to natural behavior and physiology (ibid: 183).

Effectiveness and Reversibility

Effectiveness

Sterilization is virtually 100% effective.

Population Size Reduction

Surgical sterilization may reduce deer populations (Jason R. Boulanger et al., 2012, p. 274). Theoretical models suggest that somewhere between 50% on the low end and 80% on the high end of deer need to be sterilized to successfully reduce deer populations (ibid: 275). Some deer populations may have high levels of immigration, which reduces the effectiveness of surgical sterilization (ibid: 275). With high levels of immigration, surgical sterilization is likely to be more expensive and to slow growth without reducing populations (ibid: 275-276). In one high-immigration deer population, surgical sterilization had no effect on abundance (J. R. Boulanger & Curtis, 2016). Compared to culling, sterilization is more expensive and less effective, and may be totally ineffective in large or high-immigration populations (Jason R. Boulanger et al., 2012).

In mice, ovariectomy and tubal ligation had identical effects on population growth (Chambers, Singleton, & Hinds, 1999, p. 587). At least for mice, the changes in hormones produced by an ovariectomy do not cause non-sterilized mice to reproduce more (ibid: 587).

Reversibility

Gonadectomy is irreversible.

As of yet, there is no way to reversibly occlude the oviducts (Asa & Porton, 2005, p. 33).

Vasectomy may be reversible with a relatively high success rate (Asa & Porton, 2005, p. 42). Vasectomies are more likely to be reversible if the vasectomy is done with an eventual reversal in mind (ibid: 42-43). Injecting a sclerosing agent into the vas deferens is more likely to be reversible but less effective, while injecting it into the cauda epididymis is irreversible but more effective (ibid: 43).

Physical Health Effects

Surgical sterilization is generally not preferred for wildlife contraception for practical reasons, including mortality, morbidity, irreversibility, and the difficulty and costs of catching and anesthesia (Gray & Cameron, 2010, p. 46).

Body Condition

Surgical sterilization improves body condition in rabbits (Twigg et al., 2000). Surgically sterilized female brushtail possums ovulate outside of the breeding season (Ji, Clout, & Sarre, 2000). The prolonged breeding activity caused by surgical sterilization worsens male body condition (ibid).

Reproductive System Effects

In some species, ovariectomy may improve health outcomes (Asa & Porton, 2005, p. 32). In carnivores, even endogenous reproductive hormones may cause uterine infection and tumors (ibid: 32). In dogs, an ovariohysterectomy does not improve health outcomes compared to an ovariectomy (ibid: 32).

In felids and other carnivores that have induced ovulation followed by pseudopregnancy (hormonal shifts associated with pregnancy despite the nonexistence of a fetus), vasectomy is inappropriate (Asa & Porton, 2005, p. 43). Pseudopregnancy leads to long-term elevated levels of progesterone, which leads to uterine and mammary pathology (ibid: 43).

Surgical Complications

In most species, anesthesia and surgery present risks that wildlife managers generally consider to be acceptable (Asa & Porton, 2005, p. 77). For example, post-handling mortality for surgically sterilized deer was 3%, with a range from 0% to 4% across study sites (Evans, DeNicola, & Warren, 2016, p. 3). Two mortalities were attributable to surgical complications, one to predation, one to acidosis, 1 to euthanasia because of a broken femur during capture, and 7 had inconclusive causes of death (ibid: 3).

Anesthesia may cause health problems in species such as giraffes, elephants, hippopotamus, pinnipeds, and cetaceans (Asa & Porton, 2005, p. 77). Surgery carries a high risk of complication in some species due to details of their biology: for example, cetaceans have dense blubber and a completely aquatic life history which makes surgery difficult (ibid: 77). About 10% of castrated horses experience some sort of complication, including swelling, infection, fluid accumulation, and hemorrhage from the spermatic artery (National Research Council et al., 2013, p. 123).

Disease Transmission

Sterilization may be an effective tactic for reducing disease transmission through reducing the birth rate and thus the host population (Tuyttens & Macdonald, 1998b). Sterilization is most likely to prevent diseases where the contact rate and likelihood of transmitting a disease decrease linearly with population, infected animals die quickly, nutritional stress and/or reproductive investment increase the likelihood of disease, reducing the juvenile: adult ratio reduces the rate of disease transmission, or there is a threshold density for disease transmission which is relatively close to the current density (ibid: 706).

Surgically sterilized female brushtail possums ovulate outside of the breeding season (Ji et al., 2000). Surgical sterilization of brushtail possums increases Leptospira interrogans (a bacterial infection) transmission rates, because if the normally solitary possums mate more they are more likely to transmit diseases (Caley & Ramsey, 2001). However, since surgical sterilization reduces density, the overall prevalence of the disease decreased (ibid). Another study found that surgically sterilizing both male and female possums reduced L. interrogans transmission rates (D. Ramsey, 2007, p. 114).

Male brushtail possums who have had a gonadectomy are less likely to contract bovine tuberculosis, but female brushtail possums who have had a gonadectomy are, puzzlingly, more likely to contract it (D. S. L. Ramsey, Coleman, Coleman, & Horton, 2006). Overall, there is no effect (ibid). Since sample sizes were fairly small, this outcome may not be a true treatment effect (ibid: 220-221).

Survival

Surgical sterilization increases survival of both adult and juvenile rabbits (Twigg et al., 2000) and of adult female brushtail possums (D. Ramsey, 2005). Surgically sterilized female brushtail possums ovulate outside of the breeding season (Ji et al., 2000). The prolonged breeding activity caused by surgical sterilization may increase male mortality (ibid).

Miscellaneous Health Effects

In some species, ovariectomy may improve health outcomes (Asa & Porton, 2005, p. 32). Individuals or species with a predisposition towards diabetes mellitus may also benefit (ibid: 32). Not enough data has been collected on the possible negative health outcomes of ovariectomy, such as the possibility of bone density loss in long-lived species such as great apes (ibid: 32). In dogs, an ovariohysterectomy does not improve health outcomes compared to an ovariectomy (ibid: 32).

Psychological Effects

Capture, which is necessarily for surgical sterilization, is typically highly stressful for the animal (Tuyttens & Macdonald, 1998a, p. 342).

Surgical sterilization had little effect on coyote pair bonding or territorial behavior (Gray & Cameron, 2010, p. 49).

Surgical sterilization does not alter range size in female brushtail possums (D. Ramsey, 2007, p. 14). However, surgically sterilized males had smaller ranges (ibid).

Male castration may reduce aggression, although animals who have learned to be aggressive may continue to be so (Asa & Porton, 2005, p. 42). In harem species, castrated animals may be supplanted by intact animals (National Research Council et al., 2013, p. 123).

Typical side effects of ovariectomies include decreased activity and weight gain (National Research Council et al., 2013, p. 99).

Reproductive Effects

Sexual Development

Male castration may result in the loss of secondary sexual characteristics, such as lions' manes, or the disruption of seasonal cycles in secondary sexual characteristics, such as deer antlers staying velvet (Asa & Porton, 2005, p. 42). While libido may stay the same or only decline a little, particularly in sexually experienced males, males may not achieve erection or be able to successfully copulate (ibid: 42).

Sex

Tubal ligation in deer does not alter normal hormonal functioning, leading to repeated estrus cycling (Jason R. Boulanger et al., 2012, p. 276).

In most species, ovariectomy prevents estrus and mating behavior (National Research Council et al., 2013, p. 99). However, this is not true in horses (ibid: 99).

Pregnancy

In horses, ovariectomy within the first few months of pregnancy results in a miscarriage (National Research Council et al., 2013, pp. 98–99). A pregnant doe who receives a tubal ligation will carry her fetus to term, but will not get pregnant again (Jason R. Boulanger et al., 2012, p. 276).

Practical Issues

Capturing animals for sterilization is expensive, time-consuming, and difficult, so surgical sterilization is not generally preferred among people who use contraception to manage wildlife populations (Tuyttens & Macdonald, 1998a, p. 342).

Synthetic Hormones

Synthetic hormones bind to endogenous hormone receptors and disrupt folliculogenesis, ovulation, and implantation in females and spermatogenesis in males (Giovanna Massei & Cowan, 2014, p. 3). They are widely used in zoo animals (ibid: 3). There are several kinds of synthetic hormones, including progestins (norgestomet implants, melengestrol acetate, levonorgestrel) and GnRH agonists (ibid: 3).

Progestin-based birth controls interfere with many steps of the reproductive process, including inhibiting the surge of luteinizing hormone that leads to ovulation, thickening cervical mucus to interfere with sperm entering the uterus, preventing sperm and ova from moving in the uterus, and preventing implantation (Asa & Porton, 2005, p. 33). They are perhaps the single form of wildlife contraception most often used in zoos (ibid: 33). Melengestrol acetate (MGA) is widely used in zoos and is effective for virtually all mammalian taxa in which it was tried (Asa & Porton, 2005, p. 35), including primates, ungulates, and carnivores (Giovanna Massei & Cowan, 2014, p. 3). However, it may cause uterine pathology, stillbirth, and infant mortality (Giovanna Massei & Cowan, 2014, p. 3).

Estrogens suppress follicle growth and thus prevent ovulation (Asa & Porton, 2005, p. 35). They have serious side effects, such as bone marrow suppression, aplastic anemia, uterine disease and ovarian tumors (ibid: 35-36). For this reason they are unacceptable as a form of contraception (ibid: 36). To produce a safer form of birth control, an estrogen may be combined with a progestin (ibid: 36). Among humans in America, estrogen-progestin contraceptives are the most commonly used form of contraceptive (ibid: 36).

Androgens are effective contraceptives in females, but may cause clitoral hypertrophy, vaginal discharge, male secondary sexual characteristics (e.g. manes in lions) and behavior (e.g. mounting), and aggression (Asa & Porton, 2005, p. 37). For this reason androgens are not recommended for use in wildlife (ibid: 37).

GnRH (gonadotropin-releasing hormone) stimulates production and release of follicle-stimulating hormone and luteinizing hormone and thus plays an important role in reproduction (Giovanna Massei & Cowan, 2014, p. 3). GnRH agonists mimic GNRH, but take longer to dissociate from GnRH receptors than the natural hormone does (ibid: 3). Thus, there is a brief “flareup”, stimulating semen production in males and estrus in females, followed by a long period of infertility (ibid: 3). GnRH agonists may be effective across a wide variety of taxa, including bovids, marsupials, ungulates, felids, and canids (ibid: 3). The effectiveness of GnRH agonists depends on dose rate, duration of treatment, type of agonist, and release system (ibid: 3). Side effects are similar to those of gonad removal; GnRH agonists should not be used during the breeding season as they cause abortion (ibid: 3). GnRH agonists are reversible and show no effect on lactation (ibid: 3).

Steroid hormonal contraception is generally not preferred for contraception in free-ranging wildlife, because of a variety of practical and welfare difficulties (Jay F. Kirkpatrick et al., 2011, p. 41).

Effectiveness and Reversibility

Effectiveness

In apes, levonorgestrel implants have a higher variance of duration than they do in humans, suggesting a need for conservativism about when the implant is replaced (Asa & Porton, 2005, p. 132). There is no consensus on the dose or intervals of medroxyprogesterone acetate (MPA) injections in primates (ibid: 132-133).

In captivity, melengestrol acetate (MGA) is one of the most commonly used contraceptives in ungulates (Asa & Porton, 2005, p. 150). It is highly effective in all species except hippos and the Equidae family (ibid: 150-151). MPA injections are the second most commonly used contraceptive in captive ungulates, particularly giraffes and hippos, large animals for which anesthesia is an unacceptable risk (ibid: 155-156). Data is limited for other progestins (ibid: 153). Oral hormonal pills may be ineffective in primates, who may avoid eating the pills (ibid: 139).

GnRH agonists are effective for species including cattle, pigs, sheep, deer and wapiti (Asa & Porton, 2005, pp. 157–158). In contrast to other taxa, GnRH agonists may be ineffective in ungulate males (ibid: 163-164). There is a wide range of variation between individuals in the length of time that GnRH agonists work (Herbert & Trigg, 2005, p. 146). The variation may be a product of genetic differences, variability in doses, or differences in implant manufacturing (ibid: 146). Certain animals are non-responders to GnRH agonists (ibid: 146). Since repeated treatment and administration of higher doses do not generally cause non-responders to respond, non-responding is probably genetic (ibid: 146). Long-term use of GnRH agonists is likely to increase the prevalence of non-responding in the population.

Population Size Reduction

No hormonal contraception has gone past the testing stage in free-ranging mammals (Fagerstone, Miller, Killian – Integrative ..., & 2010, 2010, p. 16). Despite considerable effort, they have yet to be used to control the populations of overabundant species (ibid: 17).

Reversibility

GnRH agonists are generally reversible, but long-term treatment is associated with longer time to reversibility, and some reports exist of complete loss of fertility (National Research Council et al., 2013, p. 118).

Physical Health Effects

In great apes, who have similar reproductive structure and function to humans, any hormonal contraception used by humans is likely to be perfectly safe (Asa & Porton, 2005, p. 72). In other primate taxa, there may be a risk of diabetes, weight gain, and uterine problems, but this has not been sufficiently studied (ibid: 72). However, there are generally few reports of physical health problems related to MGA implants (ibid: 130-131).

In females, GnRH agonists have not been associated with any significant side effects (Asa & Porton, 2005, p. 73). GnRH agonists are considered the safest form of contraception for canids (Boutelle & Bertschinger, 2010, p. 110). In felids, GnRH agonists are not associated with any known adverse health problems other than weight gain, although it is not known if they are reversible (Munson, 2006, p. 130).

Body Condition

Progestin-treated ungulates may have lower weights, perhaps due to less grazing or an extended breeding season (Asa & Porton, 2005, p. 71). GnRH agonists do not generally have an effect on body condition (Gray & Cameron, 2010, p. 48). In elk, treatment with a GnRH agonist did not change body condition (Conner et al., 2007, pp. 2352–2353). Instead, nonpregnant females catabolized significantly more lean body mass and body fat over the winter (ibid: 2353). In felids, weight gain is a side effect of GnRH agonists (Munson, 2006, p. 130). Although the research is still uncertain, progestin-based contraception may cause weight gain in carnivores (Asa & Porton, 2005, p. 71).

Reproductive System Effects

In carnivores, progestin-based contraception may cause health issues (Asa & Porton, 2005, p. 29), particularly uterine and mammary disease (ibid: 36). In this taxa, progestin-based contraception may cause a variety of endometrial problems, including endometrial mineralization (deposition of minerals in the uterine lining), cystic hyperplasia, hydrometra (excessive fluid in the uterus) and endometrial hyperplasia (growth of the uterine lining) (Asa & Porton, 2005, p. 69; Gray & Cameron, 2010, p. 48). These conditions may cause permanent infertility (Asa & Porton, 2005, p. 69). Endometrial hyperplasia increases the animal's risk of developing endometrial lesions, such as endometrial polyps, endometritis, and pyometra, which contribute to infertility and overall poor health (ibid: 70). Felids on progestins are also more likely to contract endometrial cancer, mammary cancer, and possibly benign smooth muscle tumors (ibid: 70). Progestin treatment may fail to suppress folliculogenesis or ovulation, which increases the animal's hormone exposure (ibid: 70). Estrogen-progestin based contraception is far riskier than progestin-based contraception, because the effects are synergistic (ibid: 36). The effects may be minimized by beginning hormonal treatment in deep anestrus (ibid: 36).The research has been performed mostly on felids, with some research on canids (ibid: 29).

It is unknown if progestin-based contraception increases ungulates' risk of endometrial hyperplasia, hydrometra, or uterine infections (Asa & Porton, 2005, p. 71).

GnRH agonists change ovarian follicle weight, number, and size (Gray & Cameron, 2010, p. 47).

Miscellaneous Health Effects

Some forms of progestin-based contraception may bind with other receptors and act as other steroids, causing various health problems (Asa & Porton, 2005, p. 34). It is important to choose a progestin-based contraceptive that will minimize these effects (ibid: 34).

Although the research is still uncertain, progestin-based contraception may cause weight gain and diabetes in carnivores (Asa & Porton, 2005, p. 71).

Psychological Effects

The full effect of endocrine suppression on animals' behavior and social structure is not understood (Hampton, 2017, p. 173).

Mental Health Effects

Progestin use has been linked to mood changes, lethargy, and depression in both humans and animals (Asa & Porton, 2005, p. 41). However, studies of baboons, fruit bats, tamarins and lions have found no changes in behavior (ibid: 41).

Barbary macaques treated with a progestin-based contraceptive showed higher levels of self-scratching and self-grooming; indicators of anxiety (Maijer & Semple, 2016, p. 19). They gave less and received more grooming (ibid: 19). That may also be an indicator of anxiety: macaques may seek out grooming from others to calm themselves and groom others less because they are stressed (ibid: 20). The macaques were more aggressive (ibid: 19-20). Both changes in grooming and increased aggression may disrupt macaque social structure (ibid: 20). They traveled more and rested less, but spent the same amount of time foraging (ibid: 19). Since the macaques received supplemental food from humans, the study may not have detected changes in foraging behavior (ibid: 20). The study was underpowered to detect negative psychological effects of the effect size that occurs in humans, which may mean that Barbary macaques experience more distress than humans because of hormonal contraception (ibid: 20). However, self-grooming, self-scratching, and receiving grooming from others may be successful methods of coping with anxiety, which would mean that the contraceptive has no long-term or physiological consequences (ibid: 20). Contraception may also increase skin sensitivity in monkeys, which would cause changes in these behaviors without any change in anxiety (ibid: 20).

Activity Budgets

Hormonal contraception generally does not change activity budgets (Gray & Cameron, 2010, p. 48). Levonorgestrel implants did not change the activity budgets of kangaroos (Poiani, Coulson, Salamon, Holland, & Nave, 2002, pp. 62–63). However, MGA treatment decreases time spent foraging in baboons (Gray & Cameron, 2010, p. 48). This may be positive for baboon welfare, suggesting that they struggle less with hunger.

In elk, treatment with a GnRH agonist did not have any effect on activity budgets (Conner et al., 2007, p. 2352).

Social Structure

Hormonal treatments altered elephant social structure (Gray & Cameron, 2010, p. 49).

Studies of progestin use in baboons, fruit bats, tamarins and lions have found no changes in social structure (Asa & Porton, 2005, p. 41).

Male kangaroos prefer to spend time in groups without levonorgestrel-treated females (Poiani et al., 2002, p. 64). Hormonal contraception alters lemur scent in a way male lemurs don't prefer, potentially affecting lemur social dynamics (Crawford, Boulet, & Drea, 2011). In rats, estrogen reduced investigative behavior of treated males towards untreated females, but did not affect untreated males' investigation of treated females, untreated females' investigation of treated males, or treated females' investigation of untreated males (Liu, Qin, Chen, Wang, & Shi, 2013, p. 15). Investigation may reflect the rats' social or sexual motivation (ibid: 15).

Aggression

Hormonal contraception may decrease aggressive behavior in males (Asa & Porton, 2005, p. 190). The mechanism is uncertain and may involve reduction of androgens, changes in brain mechanisms which regulate sexual behavior, changes in glucocorticoids, or the hypnotic-anesthetic effect of progestins (ibid: 190). There is considerable variance across species and studies in the effects of hormonal contraception on aggressive behavior, and more study is necessary (ibid: 190-191).

MPA may increase aggression, while MGA treatment seems not to (Asa & Porton, 2005, pp. 41–42). MPA has a high affinity for androgen receptors which may cause it to have androgen like effects on behavior (ibid: 42). In tamarins, however, MGA treatment resulted in fewer affiliative and sexual interactions and more aggression towards other females (Gray & Cameron, 2010, p. 49).

In rats, estrogen-treated females were less aggressive, while estrogen-treated males had an unchanged level of aggression (Liu et al., 2013, pp. 15–16). Control females were more likely to aggress towards treated males, perhaps because they were rejecting the males as mates (ibid: 16).

Reproductive Effects

Sexual Development

In males, GnRH agonists can cause loss of or change in secondary sexual characteristics (Asa & Porton, 2005, p. 73). For further discussion of the effects of endocrine suppression on males, see Reproductive Effects in the Immunocontraceptive Vaccines section.

It is possible that male ungulates exposed to progestin-based contraception will experience antler malformations and changes in seasonal antler development (Asa & Porton, 2005, p. 71). A few progestin-treated female lions have developed male secondary sexual characteristics such as a mane (ibid: 71).

Sex

Animals treated with progestins may continue to experience estrus cycles (Asa & Porton, 2005, p. 33). Levonorgestrel, however, appears to reduce estrus events (Gray & Cameron, 2010, p. 49). In ungulates, a longer breeding season due to progestin use may result in weight loss, increased trauma to males, and late-born fawns who die in the winter (Asa & Porton, 2005, p. 71). The effect of MGA implants on primate sexual behavior has been understudied, but it generally appears to reduce sexual behavior without eliminating it (ibid: 129). In primate species which experience a swelling around the genitalia during estrus, MGA implants generally prevent swelling, although some females may experience slight swelling (ibid: 129). Injections of MPA may or may not interfere with primate sexual behavior (ibid: 134).

GnRH agonists reduce estrus events in does, but do not reduce copulatory behavior in wapiti (Gray & Cameron, 2010, p. 49). In elk, a GnRH agonist does not change the amount of breeding behavior or cause breeding behavior to occur out of season (Conner et al., 2007, p. 2352).

In coyotes, treatment with estrogens reduces sexual behavior but does not fully suppress it. (Carlson & Gese, 2010). Other courtship and mating behavior is unchanged, the pair bond remains strong, and after estrus the treated coyotes behaved similarly to pregnant coyotes, which is called a behavioral pseudopregnancy (ibid).

Pregnancy

In some species, progestin supplementation maintains pregnancy, while in others it leads to embryo reabsorption (Asa & Porton, 2005, pp. 34–35). Estrogens appear to be safe to use in pregnancy, although cows consuming MGA during pregnancy results in low birth weight for the calf (ibid: 88). There have been cases both of progestin interfering with the animal's ability to give birth, due to its prevention of uterine contractions, and cases where an animal on progestin gave birth fine (ibid: 35). Differences may be a result of species, dosage, or type of progestin (ibid: 35). In ungulates, MGA may prevent parturition, although in some cases MGA implants during pregnancy have resulted in apparently normal parturitions (ibid: 152). Doses of progestins large enough to work as contraception may delay childbirth (National Research Council et al., 2013, p. 120). Fillies born to horses treated with progestin during pregnancy had normal reproductive development, hormone production, and fertility (ibid: 120).

Lactation

Milk production does not appear to be influenced by hormonal contraception in the few studies that have been conducted, although cats treated with progesterone may experience mammary hyperplasia (Asa & Porton, 2005, p. 35; Gray & Cameron, 2010, p. 48). Estrogens may reduce milk production and harm the development of young (Asa & Porton, 2005, p. 88). Progestins do not interfere with and may actually help milk production, and no studies have shown effects on the growth or development of young (ibid: 88). In canids, GnRH agonists prevent the initiation of lactation, although they have no effect on lactation if given after lactation has begun (National Research Council et al., 2013, p. 118).

Ecological Effects

The consequences of low-level chronic exposure to exogenous hormones through the food chain are not well understood, but may include effects on human male fertility and the human male fetus (J. Powers, 2011, p. 24). That may make steroid hormones inappropriate for any animal which humans might eat.

Immunocontraceptive Vaccines

Immunocontraception uses the animal's own immune system to prevent reproduction (Gray & Cameron, 2010, p. 45). In response to certain injections, the animal's body produces antibodies that interfere with reproduction (ibid: 45). Adjuvants– organic or inorganic chemicals, macromolecules, or cells of specific killed bacteria– are typically used to amplify the immune response (Giovanna Massei & Cowan, 2014, p. 4). The effectiveness of an immunocontraceptive vaccine is affected by species, gender, age, level of immunocompetence, delivery system, active immunogen, formulation, dose, and type of adjuvant (ibid: 4).

While immunocontraceptive vaccines against ova, sperm, and gonadotropins have been developed, the most commonly used vaccine is porcine zona pellucida, or PZP (Gray & Cameron, 2010, p. 45). PZP stimulates the production of antibodies to zona pellucida (ZP), the membrane surrounding a mammalian ovum before implantation, which prevent sperm binding to the zona pellucida sperm receptors and thus prevent fertilization (ibid: 45). The animal continues to have a normal cycle (ibid: 45). Since the structure of sperm receptors is similar across mammalian taxa, PZP is effective for a wide variety of mammalian species (ibid: 45-46). However, there are variations in ZP proteins across species, which means the same vaccine has a different level of effectiveness in each species (Giovanna Massei & Cowan, 2014, p. 4). This can be exploited to make ZP vaccines more species-specific but may also make development of vaccines for a particular species more expensive (ibid: 4). Some scholars consider ZP vaccines to deliver the best welfare outcomes of any contraceptive (Hampton, 2017, p. 183).

Vaccines against GnRH, which function similarly to GnRH agonists discussed above, are also sometimes used and cause an anestrous cycle of varied length (Gray & Cameron, 2010, p. 46). Because GnRH is common to all mammals, GnRH vaccines work in many species, including deer, elk, horses, bison, squirrels, prairie dogs, rats, swine, boar, possums, tammar wallabies, and cats (Miller et al., 2013, p. S90).

Other contraceptive vaccines have been proposed which target other aspects of hormone synthesis, ovulation, spermatogenesis, sperm or egg transport, or implantation (Jewgenow, 2017, p. 268). In domestic cats, it may be possible to use a vaccine that targets the luteinizing hormone receptor, but this has been understudied (Munson, 2006, p. 130). Vaccines that target chorionic gonadotropin, a hormone released by the placenta after implantation, have been developed but are rarely used in wildlife (J. Powers, 2011, p. 27).

Immunization trials with sperm antigens have been tried but have generally been unsuccessful (Holt, 2003, p. 294). In particular, it is possible to develop immunocontraceptive vaccines which target sperm head glycoproteins which bond to the zona pellucida (Fagerstone, Miller, Killian – Integrative ..., et al., 2010, p. 19). While it has been investigated in several species, no such vaccine has yet been developed (ibid: 19). The sperm surface is complex, with hundreds of proteins, and it is difficult to identify immunologically active proteins involved in fertilization (Holt, 2003, p. 294). It may be difficult to translate a native antigen into a synthetic antigen, some sperm antigens may be species-specific, and antibodies may not reach the female reproductive tract (ibid: 294). In addition, dozens of proteins are involved in sperm-egg interaction, and it is possible that some compensate for any particular sperm protein which is knocked out (ibid: 294).

Effectiveness and Reversibility

Unfortunately, knowledge about efficacy and treatment protocols for immunocontraceptive vaccines remains patchy (Jewgenow, 2017, p. 264). The primary focus has been on wild horses, urban deer, African elephants, and bison (ibid: 264). Immunocontraception has also been investigated for so-called "pest" species, such as small rodents like rabbits and house mice and overabundant marsupial species (ibid: 265).

Effectiveness

Both commonly used immunocontraceptive vaccines appear to be effective. For example, in wild horses, PZP vaccines led to 100% infertility in the first year, falling to 80% infertility in the third year after vaccination (Gary Killian et al., 2006, p. 68). A GnRH vaccine led to 94% infertility in the first year, falling to 53% infertility in the third year after vaccination (ibid: 68). A single-injection PZP vaccine caused 8 out of 10 does to be contracepted for 5 to 7 years each (Miller et al., 2013, p. S86). In elk, a GnRH vaccine was 100% effective in the first year, moderately effective the second year, and ineffective the third year (J. G. Powers et al., 2014). In captive exotic species, success rates of PZP have ranged from 70% in Sambar deer to 100% in addax, gerenuk, bighorn sheep, and mountain goats (Jay F. Kirkpatrick et al., 2011, p. 44).

In general, vaccines are less effective in the wild than in captivity for both elk and deer (J. G. Powers et al., 2014, pp. 653–654). Wild animals often have lower immune response than captive animals, which may be due to physiologic stress, such as poor nutritional status, parasite load, or pathogen exposure (ibid: 654). GnRH vaccines are typically less effective in wild deer populations than in captive deer populations (Miller et al., 2013, p. S92). It is hypothesized that high parasite load may reduce hosts' immune responses to vaccination (ibid: S92). This phenomenon has been noted both in humans and in animal models (ibid: S92).

Immunocontraceptive vaccines, like all vaccines, have significant variation in efficacy among different individuals (Miller et al., 2013, p. S88). Some animals will be nonresponders or have a reduced immune response (ibid: S88). In humans and companion animals, the nonresponse rate can be reduced with a booster vaccine that increases the effectiveness of the vaccine (ibid: S88). For wildlife and feral animals, a booster vaccine is not usually desirable, because it is difficult to mark animals and difficult and time-consuming to catch them more than once (ibid: S88).

GnRH vaccines have been studied in several domestic species, including sheep, pigs, cattle, horses, cats, and dogs (Jewgenow, 2017, p. 267).

While GnRH vaccines are effective in both males and females, they are typically more effective in females (Miller et al., 2013, p. S88). Male deer tend to be contracepted for two to three years from a single injection, while female deer tend to be contracepted for four to six years (ibid: S88). In female cats, the median duration of contraception from a GnRH vaccine is about forty months, while in male cats it is about fourteen months, and a quarter of male cats failed to respond at all (ibid: S88).

In the future, immunocontraceptive vaccines may become more effective. Inspired by human autoimmune diseases, researchers have been exploring ways to make proteins more immunogenic, which may lead to a new immunocontraceptive in as few as five years (Swegen, Gibb, & Aitken, 2017, p. 5).

Population Size Reduction

PZP is the only wildlife contraceptive that has been tested extensively in the field (Turner & Rutberg, 2013)S102. It has successfully limited population growth in wild populations of horses, deer, elephants, and wapiti (J. F. Kirkpatrick et al., 2009, p. 152; Turner & Rutberg, 2013, pp. S102–S103). PZP has been tested and is effective in more than eighty species, mostly ungulates (J. F. Kirkpatrick et al., 2009, p. 152), but also including equines, elephants, and some carnivores and marsupials (Jewgenow, 2017, p. 265). PZP is ineffective in the domestic cat and perhaps in some other felids (Munson, 2006, p. 130).

Immunocontraceptive vaccines take a long time to reduce population sizes. Some estimates suggest that as many as ten years of treatment may be required to cause a significant decrease in a deer herd (Warren, 2011, p. 263). However, stabilization of a wild horse population occurred within two years (Jay F. Kirkpatrick & Turner, 2008, p. 514). Immunocontraception may be more rapidly effective when used to stabilize a population at a particular size rather than to decrease a population (ibid: 514).

Reversibility

PZP has two potential mechanisms of action: “circulating antibodies which prevent interaction of the sperm and egg at fertilization and cytotoxic T-cell-mediated destruction of developing ovarian follicles” (Holt, 2003, p. 293). The latter is irreversible. However, PZP appears to be reversible even after several years of treatment, though some animals may not return to full fertility (Gray & Cameron, 2010, p. 48). Long-term treatment (>5 years) with PZP may cause ovarian failure (Asa & Porton, 2005, p. 39).

There is considerable variation among species in the duration of PZP’s contraceptive action (J. F. Kirkpatrick et al., 2009, p. 154). An annual booster is needed for speeches such as sika deer, bears, sea lions, mountain goats, and bighorn sheep (ibid: 154). Muntjac deer, zebra, and at least seventeen other species require a booster every six to nine months (ibid: 154). Sheep and goats may be infertile for as long as three or four years from a single injection (ibid: 154). PZP may cause long-term infertility in canids (Asa & Porton, 2005, p. 114).

GnRH vaccines may also result in a long-term decline in fertility (Gray & Cameron, 2010, p. 48).

Physical Health Effects

After 35 years of use, PZP has been conclusively found to be safe (Fagerstone, Miller, Killian – Integrative ..., et al., 2010, p. 23; J. F. Kirkpatrick et al., 2009, p. 153). In studies, GnRH vaccines have shown no significant health effects other than those related to reproduction (Fagerstone, Miller, Killian, et al., 2010, pp. 22–23).

There are no negative health consequences of accidentally giving an animal multiple doses of a GnRH vaccine (Miller et al., 2013, p. S91).

Body Condition

PZP improves body condition in some studies but has no effect in others, even when the same species is studied (Gray & Cameron, 2010, p. 48). PZP appears to improve body condition in horses (J. F. Kirkpatrick et al., 2009, p. 154). In deer, in general, there appears to either be no effect or a seasonal effect which quickly disappears (ibid: 154). A few deer treated with PZP have lower levels of bone marrow fat, usually depleted in severe cases of malnutrition during winter, in spite of their overall good to excellent body condition (Curtis, Richmond, Miller, & Quimby, 2007, p. 4627).

GnRH vaccines generally do not affect body condition (Gray & Cameron, 2010, p. 48). Body condition is unchanged in horses (Ransom, Powers, Garbe, et al., 2014, p. 7), cattle (Giovanna Massei et al., 2015), and prairie dogs (Yoder & Miller, 2010, p. 235). GnRH vaccination improves body condition in boar in the short term (G. Massei et al., 2008, p. 544) but not the long term (Giovanna Massei et al., 2012). White-tailed deer appear to have improved body condition, possibly related to not getting pregnant or experiencing rut, although they did not have more body fat (J. P. Gionfriddo, Denicola, Miller, & Fagerstone, 2011, p. 152). However, fox squirrels have worse body condition when treated with a GnRH vaccine, which may have been caused by their high rate of abscesses (Krause, Kelt, Gionfriddo, & Van Vuren, 2014, pp. 20–21).

Reproductive System Effects

There are concerns that the immune reaction caused by PZP vaccines might result in damage to the ovary (Asa & Porton, 2005, p. 74). PZP vaccines change ovarian follicle number, weight, and size (Gray & Cameron, 2010, p. 47). PZP treatment may result in loss of ovarian function, oophoritis (inflammation of the ovary), and cyst formation (ibid: 47). No ovarian damage has been detected in primates, horses, or deer, but damage has been detected in dogs, rabbits, mice, and sheep (J. F. Kirkpatrick et al., 2009, pp. 154–155) as well as primates (Jay F. Kirkpatrick et al., 2011, p. 44).

In deer, PZP may result in eosinophilic oophoritis (the accumulation of a certain kind of white blood cell in the ovary, causing inflammation) (Curtis et al., 2007, p. 4628). Even deer without oophoritis had a reduced number of normal secondary follicles (ibid: 4628). Eosinophilic oophoritis may be indicative of the deer having normal ovulation and successful contraception (ibid: 4628). It is unknown if these conditions cause harm to the deer (ibid: 4628).

Purified ZP proteins reduce the risk of ovarian problems related to ZP vaccines (Giovanna Massei & Cowan, 2014, p. 4).

Like PZP vaccines, GnRH vaccines change ovarian follicle number, weight, and size (Gray & Cameron, 2010, p. 47).

Injection Site Reactions

When PZP is used, injection site reactions like abscesses are uncommon (<1%), but granulomas (thickened tissue filled with fluid) are more common (Giovanna Massei & Cowan, 2014, p. 4). 89% of elephants injected with PZP had a granuloma; all granulomas were reabsorbed (Delsink et al., 2007, p. 28). 0.5%-0.7% of treated horses develop an abscess, although sterile granulomas were common (J. F. Kirkpatrick et al., 2009, p. 154). 0.5% of deer experience an abscess (ibid: 154). In zoos, across a variety of species, 1.3% of treated animals develop an abscess (ibid: 154). Remote darting may force hair follicles and surface dirt into the wound, causing an abscess even if the vaccine does not (ibid: 154). These abscesses generally drain within two weeks without long-term consequences (ibid: 154). Some deer may form granulomas at the injection site with all the characteristics of tuberculosis (Curtis et al., 2007, p. 4627). This is common in animals injected with Freund's Complete Adjuvant (ibid: 4627), which is why this adjuvant is no longer used in wildlife contraception. In felids, PZP causes local reactions which sometimes include granulomas and hypercalcemia (elevated blood calcium) (Munson, 2006, p. 130). The long-term effects of granulomas on welfare in free-living species are unknown, because many animals are not monitored long-term (Hampton, 2017, p. 171).

In some species, GnRH vaccines may cause a granuloma or sterile abscess at the injection site (Giovanna Massei & Cowan, 2014, p. 4). Some evidence suggests, however, that these granulomas and abscesses do not generally cause limping or difficulty moving (ibid: 4). Some species, such as cats, wallabies, and grey kangaroos, may be less prone to injection site reactions than others are (Miller et al., 2013, p. S92). Some species, such as dogs, may require lower doses to prevent injection site reactions (ibid: S92). Injection site reactions may be more common in the wild: for example, captive white-tailed deer never have an injection site reaction, while free-ranging white-tailed deer sometimes do (ibid: S92). Deer who have poor general health or a high parasite load may be more likely to experience an injection site reaction (ibid: S92).

In one study of elk, all injected females had subcutaneous or intramuscular lesions at the injection site, although there was no evidence of lameness, visible lesions, lesions detectable through external palpation, or detriment to overall health and fitness; these lesions lasted for at least three years (J. G. Powers et al., 2014). In another study, 35% of elk had abscesses while more had some kind of injection-site inflammatory lesion; no lameness was observed (J. Powers, 2011, p. 47). 87% of treated fox squirrels had an abscess (Krause et al., 2014, p. 18). Affected individuals had a mean of 1.6 abscesses, perhaps due to fluid accumulating in subcutaneous pockets near the injection site (ibid: 18). Open abscesses leaking pus were often noted, and treated squirrels were more likely to limp or walk stiffly (ibid: 18).

White-tailed deer did not have limps, impaired mobility, limited range of motion, or visible injection-site reactions (J. P. Gionfriddo et al., 2011, pp. 151–152). However, GnRH-treated deer were more likely to have internal granulomas and abscesses two years after injection (ibid: 152). In one study, 4 of 17 GnRH-treated deer had an intramuscular tissue reaction, including chronic abscesses and a granulomatous nodule, two years after injection (James P. Gionfriddo et al., 2009, p. 181). An additional deer had severe local lesions with signs of infection (ibid: 181). In cattle, there was no injection site reaction or limping (Giovanna Massei et al., 2015); the same was true of boars (G. Massei et al., 2008, p. 542; Giovanna Massei et al., 2012)

Survival

PZP treatment may improve animals' survival. For example, in horses, PZP treatment decreases mortality and increases longevity (J. F. Kirkpatrick et al., 2009, p. 154). In fact, PZP treatment has such an effect that many horses began to live past the age of 25, which was never seen before treatment (Gray & Cameron, 2010, p. 50).

Miscellaneous Health Effects

Few studies have examined the effects of PZP on blood chemistry (J. F. Kirkpatrick et al., 2009, p. 155). In general, treated animals' blood parameters appear to be in the normal range for their species (ibid: 155).

In cattle, GnRH vaccines do not affect size of lymph nodes or body temperature (Giovanna Massei et al., 2015). In boar, GnRH vaccines do not affect any biochemical or hematological parameters (Giovanna Massei et al., 2012). In prairie dogs, GnRH vaccines do not affect measures of liver function, kidney function, or nutritional status (Yoder & Miller, 2010, p. 235). In white-tailed deer, GnRH vaccines do not affect blood chemistry parameters (J. P. Gionfriddo et al., 2011, p. 15), although they do cause lymph node reactions, which potentially include secondary granulomatous inflammation and hyperplasia (ibid: 157). There were no effects on the organs of deer, other than smaller mammary glands, uteruses and ovaries due to not reproducing (James P. Gionfriddo et al., 2009, p. 181). In elk, GnRH vaccines did not significantly affect any blood chemistry or hematology parameters (J. Powers, 2011, p. 47).

Speculative Health Effects

Immunocontraceptives may cause certain health problems which have yet to be studied (Jewgenow, 2017, p. 271). They may disrupt endocrine function, which may disturb metabolic homeostasis and cause disease (ibid: 271). Antibodies that target sperm or egg proteins may damage gamete-producing organs (ibid: 271). Long-lived female animals that never reproduced may have uterine tumors or cysts (ibid: 271).

GnRH receptors exist throughout mammals' bodies, including in the cerebellum, bladder, and cerebrospinal fluid (Jay F. Kirkpatrick et al., 2011, p. 43). GnRH is a neurotransmitter with effects throughout the central nervous system (ibid: 43). GnRH agonists can interfere with olfaction, which is necessary for normal animal behavior in many species (ibid: 43). Since GnRH may play a role in cardiac function, GnRH vaccines may cause cardiac problems (ibid: 43). There are concerns that GnRH vaccines may interfere with non-reproductive function of the hypothalamus and pituitary gland, although this has not been studied (Jewgenow, 2017, p. 268). The true effects of inhibiting GnRH throughout the body are unknown (Jay F. Kirkpatrick et al., 2011, p. 43).

GnRH vaccines function differently from GnRH agonists, since at no point does a GnRH vaccine result in an above-average level of GnRH (National Research Council et al., 2013, p. 115). Information about GnRH agonists may not generalize to GnRH vaccines (ibid: 115).

Psychological Effects

In general, there are few changes in behavior due to PZP, and most of them are directly caused by females not being pregnant or lactating and not having foals (Ransom, Cade, & Hobbs, 2010, p. 59).

Activity Budgets

In general, PZP does not change activity budgets (Gray & Cameron, 2010, p. 48). One study of horses found no change in activity budgets (Powell, 1999), while another study found that PZP-treated mares spend slightly less time feeding and more time resting and engaged in maintenance and social behaviors (Ransom et al., 2010, pp. 55–56). This effect is probably because pregnant and lactating mares feed more than other mares (ibid: 58).

Female horses treated with GnRH vaccines fed less, rested more, traveled less, and performed more maintenance behaviors than controls, but engaged in the same amount of social behavior (Ransom, Powers, Garbe, et al., 2014, p. 7). GnRH vaccines do not change activity budgets of boar (G. Massei et al., 2008, pp. 542–543). GnRH vaccines do not change feeding behavior of cattle (Giovanna Massei et al., 2015).

Social Structure

PZP may lead to fewer associations with conspecifics in white-tailed deer (Gray & Cameron, 2010, p. 49). It did not alter elephant social structure (ibid: 49).

PZP-treated mares are more likely to change harems, although it's unclear if this is because of reduced male attention to infertile mares, increased male harassment due to a longer period of estrus cycling which causes the female to switch harems, or the female's attempt to get pregnant (Madosky, Rubenstein, Howard, & Stuska, 2010; Nuñez, Adelman, Mason, & Rubenstein, 2009). In one population where mares were treated with PZP, the sex ratio became 1: 1.67 in favor of females due to the increased longevity of contracepted mares (Jay F. Kirkpatrick & Turner, 2008, pp. 516–517). PZP does not appear to change mares' spatial relationships with the stallion or level of aggression given or received (Powell, 1999). PZP does not alter the ranges or movements of female white-tailed deer (Hernandez et al., 2006).

GnRH vaccines did not alter the social hierarchies of brushtail possums (Gray & Cameron, 2010, p. 49) or wild boars (Jewgenow, 2017, p. 273). No significant changes in the behavior of squirrels were observed (ibid: 273).

Aggression

PZP may increase aggression and masculine behavior in felids (Gray & Cameron, 2010, p. 49). PZP does not appear to change mares' level of aggression given or received (Powell, 1999).

Immature male tammar wallabies treated with GnRH vaccines were less aggressive and less dominant (Hampton, 2017, p. 173). GnRH vaccines can be used to reduce aggression in male elephants, particularly aggression related to musth, a frenzied state male elephants enter into during the rutting season (Bertschinger et al., 2005, pp. 15–16).

Reproductive Effects

Sexual Development

Immature males treated with GnRH vaccines and other forms of endocrine suppression are generally smaller than untreated males and may have increased fat deposition (Hampton, 2017, p. 172). Especially in juveniles, sex-specific phenotypes fail to develop and males become 'feminized,' often permanently (ibid: 172). Other sex-specific processes such as antler shedding may be disrupted (ibid: 172). In bucks, GnRH vaccine treatment causes loss of masculine appearance and prevents development of antlers and testicles (G. J. Killian & Miller, 2000, p. 287).

Sex

Preventing natural reproductive behavior, such as courtship and mating, may cause harm to animals, because courtship and mating are generally very pleasurable (Hampton, 2017, p. 174).

In deer, boar, and horses, GnRH vaccines prevent reproductive behavior such as estrus cycles (Gary Killian, Wagner, Fagerstone, & Miller, 2008; Miller et al., 2013, p. S88). GnRH-vaccine-treated does do not experience repeated estrus cycles, an extended breeding season, or late fawning (G. J. Killian & Miller, 2000, p. 287). GnRH-vaccine-treated does show no signs of sexual libido and bucks do not attempt to mount them (ibid: 287). GnRH-vaccine-treated bucks show no interest in sex (ibid: 288). However, GnRH-vaccinated female elk perform precopulatory behavior for a longer time period than unvaccinated female elk do, and males are more likely to direct precopulatory behavior towards them (J. Powers, 2011, p. 50). There are no differences in general reproductive behavior (ibid: 50).

A return to breeding behavior is typically observed before a return to fertility (Miller et al., 2013, p. S88). It is believed that this is because GnRH vaccines control luteinizing hormone more effectively than they control follicle-stimulating hormone (ibid: S88). Thus, sufficient follicle-stimulating hormone is released to induce signs of estrus, but insufficient luteinizing hormone is produced to cause ovulation (ibid: S88).

Immature male tammar wallabies treated with GnRH vaccines experienced sexual interest from untreated males (Hampton, 2017, p. 173).

PZP-treated females received many more reproductive behaviors, probably because of increased estrus (Ransom et al., 2010, p. 58).

Unlike GnRH agonists, GnRH vaccines do not induce estrus, semen production, or ovulation (Herbert & Trigg, 2005, p. 148).

ZP proteins do not cross-react with other tissues and protein hormones (Jay F. Kirkpatrick et al., 2011, p. 42). Therefore, they are “downstream” of many reproductive processes, leaving the animals with reproductive behavior as natural as possible (ibid: 42). However, PZP-treated white-tailed does have more estrous cycles than untreated females and may remain sexually active after the end of the usual breeding season (Gray & Cameron, 2010, pp. 48–49; G. J. Killian & Miller, 2000, p. 286; Miller et al., 2013, p. S87). A PZP-treated doe has a mean of 2.4 cycles, lasting 98 days (Miller et al., 2013, p. S87). PZP-treated does may have a breeding season of as many as 150 days, while untreated does have a breeding season of only 40 days (G. J. Killian & Miller, 2000, p. 287). PZP also extends the breeding season for wild horses (Nuñez, Adelman, & Rubenstein, 2010). The same dynamic may apply to PZP-treated animals more generally (Asa & Porton, 2005, p. 75).

In ungulates, persistent estrus may lead to weight loss, while in carnivores it may result in pathological exposure to reproductive hormones, similar to what was discussed in the hormonal contraception section (Asa & Porton, 2005, p. 75). If PZP wears off late in the season, a fawn may be born in July or August, putting it at serious risk of overwinter mortality (G. J. Killian & Miller, 2000, p. 287). PZP treatment results in later births for wild horses (Nuñez et al., 2010). The increase in estrous cycles may also lead to more movement and disruption of social hierarchy, although some studies found no change in social behavior (Giovanna Massei & Cowan, 2014, p. 4). Repeat estrus may, in some species, result in increased aggressive, following, or chasing behavior on the past of males, with deleterious health consequences (Asa & Porton, 2005, p. 77).

Pregnancy

PZP vaccines are safe in pregnancy (J. F. Kirkpatrick et al., 2009, p. 153). Pregnant female mares treated with PZP produce healthy, fertile foals who are as likely to survive as foals with untreated mothers (ibid: 153). It is also safe for pregnant elephants and deer (ibid: 153-154).

GnRH vaccines are safe in pregnancy in all species in which they have been tested, including deer, elk, bison, and horses (Miller et al., 2013, p. S91). However, the safety of GnRH vaccines in pregnancy is likely to be species-specific (Jay F. Kirkpatrick et al., 2011, p. 43). In species that rely on pituitary luteinizing hormone to maintain the corpus luteum, GnRH vaccines may cause abortion (ibid: 43).

GnRH vaccination of female elk does not affect their calves' survival rate or weight (J. Powers, 2011, p. 38). Passive transmission of GnRH antibodies during the first sixty days of life has no effect on elk reproductive development, semen quality, fertility, or secondary sexual characteristics (ibid: 70-75).

Evolutionary and Ecological Effects

Immunocontraceptive vaccines could result in natural selection for individuals that remain fertile because of no or low response to vaccination or compromised immune function (Asa & Porton, 2005, p. 75; Cooper & Larsen, 2006, pp. 823–825; Giovanna Massei & Cowan, 2014, pp. 12–13). Inbreeding among a small number of nonresponders, especially if nonresponse is a product of a single genotype, may reduce genetic variability (Cooper & Larsen, 2006, p. 826; Magiafoglou, Schiffer, Hoffmann, & McKechnie, 2003, p. 155). Depending on how heritable response to immunocontraceptive vaccines is, it may be possible to select for decreased immune function within only a few generations, potentially placing animals at risk of illness (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 265). Conversely, if variation in immunocontraceptive effectiveness is primarily due to the environment, even huge amounts of immunocontraceptive use will have little effect on future generations (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 265).

Evidence suggests immune function is heritable (Ransom, Powers, Thompson Hobbs, et al., 2014, p. 265). However, immune function is only one component of fertility effects, and underlying components of traits typically have higher heritability than traits themselves (Magiafoglou et al., 2003, p. 153). Natural situations are more stressful and more variable than laboratory situations, in which immune response is most often studied, so nonresponse will be less heritable (ibid: 153). Whether nonresponse to immunocontraception will evolve depends on selection intensity, the frequency of genetic variants, and how genetic variants affect the phenotype: for example, low selection intensity means the spread of a particular gene is not favored very strongly, while very high selection intensity may mean the species is driven extinct before resistance evolves (ibid: 154). Immigration from non-immunized sources may lower the frequency of resistant individuals and limit adaptation (ibid: 154). While immunocontraception resistance probably trades off against something, it is currently uncertain what the fitness costs of immunocontraception resistance are and whether they would prevent it evolving (ibid: 155). Nonresponse appears to be heritable in brushtail possums (Holland, Cowan, Gleeson, Duckworth, & Chamley, 2009).

It is important to monitor the heritability of nonresponse to immunocontraception in both the laboratory and the field (Giovanna Massei & Cowan, 2014, p. 13; Ransom, Powers, Thompson Hobbs, et al., 2014, p. 265). We may also reduce the selective pressure on animals, perhaps by allowing each female to have one child before using contraception or only contracepting a percentage of the population (Ransom, Powers, Thompson Hobbs, et al., 2014, pp. 265–266). Immunocontraception may work best on species with long generation times, where adaptation will take decades or longer (Cooper & Larsen, 2006, p. 825). A multi-vaccine approach may slow the rate of resistance evolving (Magiafoglou et al., 2003, p. 156).

In most species, a certain percentage of the population does not respond to GnRH vaccines (Herbert & Trigg, 2005, p. 148). If only nonresponders breed, there would be a considerable degree of natural selection for nonresponse, which would limit the lifespan of the vaccines (ibid: 148).

In one study, over the course of thirteen years of treatment with PZP, there was no loss of genetic diversity (Jay F. Kirkpatrick & Turner, 2008, pp. 517–518).

No immunocontraceptive vaccine enters the food chain or poses a risk to animal or human predators (Giovanna Massei & Cowan, 2014, p. 5). The vaccines are broken down as soon as they're ingested (ibid: 5).

Practical Issues

PZP vaccines are derived from the ovaries of pigs slaughtered in slaughterhouses (Miller et al., 2013, p. S87). For this reason, many animal rights advocates may consider the use of PZP to be unethical. ZP vaccines can be derived from bacteria, but they are generally less effective (ibid: S87).

GnRH vaccines may be popular among humans because they suppress animals' sexual behavior, which may be a nuisance in species that interact closely with humans (Jewgenow, 2017, p. 267).

Immunocontraception, like other contraceptives, is generally socially acceptable. In one study, over 90% of respondents considered immunocontraception to be an acceptable and humane form of gray squirrel population control (Barr, Lurz, Shirley, & Rushton, 2002, p. 345). Respondents generally considered immunocontraception to be more acceptable and humane than any other option for gray squirrel control, including poisoning, trapping, and shooting (ibid: 345).

In elephants, rotational immunocontraception has been used to reduce population sizes (Druce, Mackey, & Slotow, 2011). Rotational immunocontraception means that one elephant is permitted to be fertile in each family group; once it calves, it is given an immunocontraceptive vaccine, and another elephant is allowed to become fertile (ibid). Rotational immunocontraception increases the inter-calving interval while meeting the group's social need for a child to be born into the group on a regular basis (ibid). Compared to no contraception, in elephants, rotational immunocontraception halves the population's growth rate and doubles its doubling time (ibid). While rotational immunocontraception is too resource-intensive for most species, it may be an appropriate tool for large, social mammals with high moral weight (e.g. elephants, dolphins, primates).

Other Contraceptives

Nonsurgical Sterilization

Some work has been done on nonsurgical sterilization (Hall, Nixon, & Aitken, 2017). Nonsurgical sterilization would not require readministration, unlike all currently developed forms of contraception (ibid: D). One method for nonsurgical sterilization involves targeting non-renewable germ cells, which unlike eggs and sperm are not replenished, by creating a localized state of oxidative stress within the gonad (ibid: D). Another strategy involves generating autoantibodies which target eggs or sperm, leading to reproductive failure (ibid: E). A third strategy involves interfering with the mother's body's ability to recognize that it is pregnant, preventing implantation (ibid: E-F).

Oral forms of non-surgical sterilization are currently under development (Humphrys & Lapidge, 2008, pp. 580–581). These may target gonadotrophs in the brain or primordial follicles in the ovary (ibid: 580-581).

There is currently no nonsurgical sterilization method which is ready for use on actual animals. However, nonsurgical sterilization may be cheaper and more effective than other forms of animal contraception, permit the sterilization of both females and males, and have a more positive effect on animal welfare (Hall et al., 2017, p. F–G). It is unknown how nonsurgical sterilization would affect survival rates, social structure, and behavior, whether animals would evolve to be resistant, and whether the contraceptive agent would pass from waste into land and water systems (ibid: F-G).

ContraPest

ContraPest is a liquid fertility control bait for rats which has recently become available and which impairs spermatogenesis in males and ovulation in females (Siers et al., 2017, p. 1). ContraPest contains two chemicals, 4-vinylcyclohexene diepoxide and triptolide (ibid: 1).

The compound 4-vinylcyclohexene diepoxide increases the rate of follicular atresia, destroying primary and primordial follicles, depleting the ovary of most existing follicles, and causing ovarian senescence (Fagerstone, Miller, Killian – Integrative ..., et al., 2010, p. 17). Treated females have similar hormonal profiles to females going through menopause (ibid: 17). Ten days of treatment has some effect, and the effect is complete after thirty days of treatment (ibid: 17). It is being explored for use in dogs and cats (ibid: 17), in addition to its use in rats.

Triptolide is the active ingredient in the traditional Chinese medicinal herb Tripterigygium wilfordii (Witmer et al., 2017, p. 81). It lengthens the interval between estrous cycles and increases the amount of apoptosis (normal cell death) in ovarian secondary follicles (ibid: 81). It may inhibit the expression of estrogen-synthesizing enzymes (ibid: 81). It causes infertility in male rats (ibid: 81).

If rats are provided with ad libitum access to baits, under laboratory conditions, beginning two weeks before mating and continuing throughout the entire first breeding cycle, ContraPest successfully prevents breeding for two breeding cycles (Siers et al., 2017, p. 6). It reduces litter size during the third breeding cycle, but has no effect on the fourth breeding cycle (ibid: 6). Wild-caught rats willingly consume the bait (Witmer et al., 2017, p. 87). ContraPest has no effect on rats' adrenal, kidney, spleen, or liver weights, indicating a lack of side effects (Witmer et al., 2017, p. 89).

Treatment with VCD alone decreases bone mineral density (Lukefahr et al., 2012). There is no effect of VCD-only treatment on body weight, but VCD-treated rats eat less when food is provided ad libitum (Muhammad et al., 2009, pp. 48–49). For peripubertal rats, there is no effect of VCD treatment on hematology parameters, but for adult rats VCD treatment increases neutrophil counts and decreases hemoglobin and hematocrit, consistent with inflammation (ibid: 52-53). Peripubertal rats appear to retain normal renal function, while adult rats had significant increases in creatinine and blood urea nitrogen, which suggests a loss of renal function (ibid: 53). All rats retained normal liver function but had heavier livers (ibid: 53-54). VCD does not appear to cause generalized toxicity outside of the ovary (Mayer, Devine, Dyer, & Hoyer, 2004). In high doses, VCD is carcinogenic causing forestomach hyperplasia, adenomas and carcinomas, ovarian neoplasms and death (Burd, 2014)24. However, much smaller doses are required for ovarian senescence (ibid: 24). High-dose VCD treatment may cause vomiting for brushtail possums (ibid: 46). In brushtail possums, VCD does not appear to cause liver toxicity or changes in hematological parameters (ibid: 47-48).

Treatment with VCD alone causes female rats to show signs of anxiety and reduces their levels of progesterone, plasma testosterone, and plasma DHT (Reis et al., 2014). Treatment with VCD alone does not affect amount of time spent wheel running, average speed, or maximum speed (Perez et al., 2013).

There is no risk of bioaccumulation with ContraPest, because the active compounds have a very short half-life (Swegen et al., 2017, p. 5). ContraPest is species-specific and safe for human handling because of the low concentrations of its active ingredients and design of its proprietary bait stations (ibid: 5). Therefore, it would probably not be species-specific if used in greater quantities on larger mammals (ibid: 5). Mammalian species which are similarly sized to rats may be targeted if ContraPest is deployed in a suburban or rural environment, in which these species are more common (ibid: 6).

Intrauterine Devices

IUDs prevent pregnancy using local mechanical effects on the uterus which prevent implantation (Asa & Porton, 2005, p. 40). Most devices include an electrolytic copper coating, which is spermicidal (ibid: 40). IUDs have been developed for humans (which may also work for great apes and other primates), cows, ewes, goats, and domestic dogs (ibid: 40-41).

In wild horses, intrauterine devices (IUDs) lead to 80% infertility in the first year, falling to 14% infertility in the third year (Gary Killian et al., 2006, p. 68). Horses may lose their IUDs (ibid: 68). While in humans IUDs are rarely expelled, nonhuman mammal uteri vary considerably and expulsion may be more common (Asa & Porton, 2005, p. 57). If the long tails on an IUD are not cut, the animal may remove the IUD (ibid: 57).

IUDs may cause uterine inflammation (Gray & Cameron, 2010, p. 48). However, they do not cause uterine inflammation in wild horses (Gary Killian et al., 2006, p. 70).

In some species, IUDs suppress the estrous cycle, which means they may have a different mechanism of action than the mechanism in humans (Asa & Porton, 2005, pp. 40–41).

Birds

The simplest form of contraception for birds is addling the eggs, such as by shaking or oiling them (Fagerstone, Miller, Killian – Integrative …, et al., 2010, p. 17). However, this method is too labor-intensive to be practical in any but the smallest areas (ibid: 17).

Ornitrol, a cholesterol mimic, prevents the formation of the steroid hormones testosterone and progesterone (Fagerstone, Miller, Killian – Integrative …, et al., 2010, p. 17). Its effects last for several months (ibid: 17). While registered in the 1960s for oral use in pigeons, its registration was canceled in 1993 (ibid: 17). Pigeons are year-round breeders, which increased both the expense and the health risks of Ornitrol use (ibid: 17). It is also effective in quail, and may be effective in many bird and mammalian species (ibid: 17-18). Ornitrol may be useful in seasonally breeding birds (ibid: 18). It may pose serious health consequences if fed for extended periods (ibid: 23).

Conjugated linoleic acid (CLA) may be effective in cold climates (Fagerstone, Miller, Killian – Integrative …, et al., 2010, p. 18). At temperatures about as cold as a refrigerator, CLA leads to the solidification of egg yolks, preventing hatchability (ibid: 18). Since birds do not generally incubate their eggs until the last egg is laid, there is plenty of time for CLA to work (ibid: 18). It needs to be fed for ten days or longer (ibid: 18). Perhaps for this reason, it was found ineffective in a limited field trial in Canada geese (ibid: 18). It is reversible (ibid: 18).

Nicarbazin (NCZ) is a bird-specific oral contraceptive (Giovanna Massei & Cowan, 2014, p. 5). It disrupts the membrane between the yolk and the egg albumen, compromising fetal development (ibid: 5). The effect on fertility is reversible and it poses minimum risk to scavengers and predators (ibid: 5). NCZ permits birds to engage in ordinary egg-laying and incubation behavior (Fagerstone, Miller, Killian – Integrative …, et al., 2010, p. 18). It is safe in both target and non-target bird species, even when fed at far higher doses than required for the contraceptive effect, and has no effect on mammals (ibid: 23). However, NCZ must be fed continuously before and during egg-laying, which may cause its equivocal results in the field (Giovanna Massei & Cowan, 2014, p. 5). It has an astringent taste that many birds find aversive, which complicates oral delivery (Fagerstone, 2002, p. 10).

NCZ, CLA, and Ornitrol pose minimal risks to humans who consume birds who use the contraceptives (Fagerstone, Miller, Killian, et al., 2010, p. 23).

MPA, a progestin, has been used successfully in captive parrots (Asa & Porton, 2005, p. 230).

Miscellaneous

Several contraceptives are in the early phase of development, including GnRH-toxin conjugates and cholesterol mimics (Giovanna Massei & Cowan, 2014, p. 5). GnRH-toxin conjugates selectively kill cells which secrete reproductive hormones, possibly causing sterility (ibid: 5). Cholesterol mimics inhibit production of cholesterol, which is a parent compound of male and female reproductive steroids (ibid: 5). Cholesterol mimics have a small window between their effective dose and the dose that causes undesirable physical and behavioral side effects (ibid: 5). They bioaccumulate, which means they could be dangerous to predators or scavengers (ibid: 5). Cholesterol mimics are probably inappropriate for free-ranging wildlife contraception (ibid: 5). Some researchers are also targeting the mammalian ovary to induce early menopause and permanent sterility (ibid: 5-6).

The bisdiamine compounds, which target the male germinal epithelium (the innermost layer of the testicle), appear to be safe, effective, and reversible in felids (Munson, 2006, p. 131). However, they lower serum testosterone levels, which may lead to behavior changes and loss of secondary sexual characteristics (ibid: 131). As bisdiamines are teratogens in felids, it must not be delivered to female felids (ibid: 131).

A variety of plant extracts may be useful contraceptives for female rodents (Tran & Hinds, 2013). These may be ecologically safe and unlikely to pass up to the next trophic level (ibid: 10). Plant extracts may also be cost-effective, particularly if prepared locally by farmers (ibid; 10). However, they may be labor-intensive to deliver, because they need to be fed daily, and generally don’t taste very good, potentially reducing uptake (ibid: 10).

Ornidazole, an antibiotic and antiprotozoal drug, causes infertility in rats by inhibiting sperm glycolysis (breakdown of sugars) and mobility (Swegen et al., 2017, p. 6).

Delivery Methods

Delivery methods are one of the thorniest issues regarding wildlife contraception. Arguably, the greatest problem of wildlife contraception is not developing a functional contraceptive but developing a contraceptive that functions when delivered remotely, in a cost-effective way, to a large population (Holt, 2003, p. 286). There are a variety of methods for delivering contraceptives, including direct injection, subcutaneous implants, remote delivery systems, oral consumption, and live organisms (Giovanna Massei & Cowan, 2014, p. 6).

Implants

Subcutaneous implants deliver fertility control drugs to the animal’s bloodstream over a period of time (Giovanna Massei & Cowan, 2014, p. 6). Implants may be used with both steroid hormonal contraception and GnRH agonists (Asa & Porton, 2005, p. 44).

Implants may break or be lost inside the body, although using appropriate surgical techniques minimizes this risk (Asa & Porton, 2005, pp. 44–45).

Since implants require individual handling of each animal, they are not practical for most purposes (Asa & Porton, 2005, p. 46). The use of implants is inappropriate in free-ranging primates, who may remove the implant due to their inquisitive nature (ibid: 144). In zoos, it is recommended that primates who have had an implant be separated from their social group for five to seven days, a recommendation that causes social problems, stresses the animal, and is impractical for free-ranging wildlife (ibid: 144). Implants may be suitable for small urban mammals, such as skunks and raccoons, where capture is easy and the chance of passing contraceptives through the food chain is low (ibid: 213). (If the risk of passing contraceptives through the food chain is high, a contraceptive that is not passed along when the animal is eaten, such as immunocontraception, should be used.)

Capture, restraint, and handling is generally stressful to animals and causes suffering (Hampton, 2017, p. 169). A study of implants in horses was suspended because the surgery was invasive and caused unacceptable levels of stress to mares (National Research Council et al., 2013, p. 120).

Remote Delivery

Remote delivery systems include bio-bullets (biodegradable projectiles) and syringe darts (Giovanna Massei & Cowan, 2014, p. 6). Remote delivery systems can be used to deliver vaccines or injectable depot preparations, which may release either steroid hormones or GnRH agonists (Asa & Porton, 2005, p. 44).

Remote delivery systems target individual animals, allow for tailoring the dose based on bodyweight, can deliver both solid and liquid formulations, and avoid the cost and labor involved in trapping (Giovanna Massei & Cowan, 2014, p. 6). However, some individuals may be vaccinated multiple times, receive the wrong dose, or fail to complete the injection (ibid: 6). Even darts that fire properly may fail to inject their contents into the muscle (Asa & Porton, 2005, p. 57). Most contraceptives are fairly harmless if delivered multiple times, but multiple deliveries of progestins may produce side effects like immunosuppression (ibid: 57). In some cases, the amount of medication that needs to be injected is larger than the amount that can be practically delivered (ibid: 84). Species with thick skin or subcutaneous fat layers may need very long needles (ibid: 84-85). Some contraceptives, such as some forms of PZP, become too viscous to be injected when the weather is cold (ibid: 84).

Many methods have been used in practice to deliver contraceptives. Wild horses are vaccinated with PZP during routine roundups for other management purposes (Turner & Rutberg, 2013, pp. S103–S104). Remote darting from a helicopter has also been used on wild horses, but it is typically not used because it is expensive and potentially dangerous due to the necessity of low flying and offers no guarantee of actually hitting the horses (ibid: S104). More practically, remote darting of wild horses can be done by trailing the horses by foot or baiting with food or water (ibid: S104). Deer can be darted using several methods, including bait stations, vehicles, and following on foot (ibid: S104). Many state wildlife agencies require ear tagging of contracepted deer, which is expensive but allows for hand delivery of contraceptives (ibid: S104). Elephants become wary of a darting vehicle, so helicopters are more appropriate (Delsink et al., 2007, p. 27). Elephants find helicopters more stressful than ground darting, but ground darting takes longer since the elephants can flee more effectively (ibid: 29). In addition, normal movement and social patterns are restored within a few days for helicopter darting, but take a few weeks for ground darting (ibid: 29).

Darted individuals must be identified to prevent double treating. Animals of some species can be individually identified, such as with a microchip, ear tag, brand, or knowledgeable human, but this is too expensive to do generally (Turner & Rutberg, 2013, p. S104). Treating an entire social group at once can allow for identification and prevent retreatment (ibid: S104). Some remotely delivered injections can leave a paint mark for several weeks to prevent retreatment (ibid: S104). Marking may cause suffering in some species: for example, in marine mammals, marking may cause pain and behavior change, including change in swimming, maternal, and foraging behaviors (Walker, Trites, Haulena, & Weary, 2011).

Any method that involves capture or remote delivery may cause the animal stress (Jewgenow, 2017, p. 271). However, remote delivery systems may minimize suffering, other than that associated with darting injuries or injection site interactions (Hampton, 2017, p. 169).

Remote delivery becomes less effective over time as animals become wary (Jewgenow, 2017, p. 271). Repeated applications also cause animals more suffering (Hampton, 2017, p. 169). Darting becomes more expensive over time, as the only untreated deer become those that were too wary to be previously treated (Rudolph, Porter, & Underwood, 2000, p. 468).

Darting is more expensive if the animals are at a low density (Rudolph et al., 2000, p. 468). In suburban regions, some land may not be accessible to darters, because of landowner opposition, vegetation, or proximity to roads or places where children play (ibid: 468).

Oral Delivery

The oral route involves placing the contraceptive in some kind of bait, which the animals will hopefully eat. It presents many difficulties. The oral route makes it difficult to control the dose each individual receives (Asa & Porton, 2005, p. 46). In many cases, contraceptives are not distributed evenly through the feed (ibid: 85). Low-status individuals may not consume a full dose because they are excluded from the feeding site (ibid: 85). Animals may refuse to eat a feed with an unusual taste or appearance (ibid: 85). In addition, the bait must be sufficiently attractive to the target species to have a population effect without attracting nontarget species (Asa & Porton, 2005, p. 46; Giovanna Massei & Cowan, 2014, p. 6). Species-specificity may be achieved through bait choice, bait delivery mechanism, or altering timing, placement, scale, distribution, or frequency of bait reapplication (Humphrys & Lapidge, 2008, pp. 581–582).

The oral route is particularly difficult for an immunocontraceptive, because the immune system has a relatively high threshold for recognizing an orally delivered antigen as “foreign” and mounting a defense (Giovanna Massei & Cowan, 2014, p. 6). For this reason, orally delivered vaccines are likely to be short-lived and require repeated applications (ibid: 6). However, there have been some successes, such as a carrot genetically engineered to express possum ZP proteins (Barlow, 2000, p. 899).

Some oral particulate delivery systems are designed to avoid digestion and stimulate the immune system (Holt, 2003, p. 298). However, these are too expensive for routine use in wildlife (ibid: 298). So-called “bacterial ghosts”, which have intact envelopes but are devoid of cytoplasmic content such as genetic material, can also be used for oral delivery (ibid: 298-299). Researchers have also used virus-like particles, lipoprotein nanoparticles which do not replicate but which resemble viruses immunologically (Cross, Zheng, Duckworth, & Cowan, 2011, p. 93). Non-disseminating but self-replicating delivery systems, such as genetically modified viruses and parasites, may be used (ibid: 94). These systems are resident longer in the body, thus exposing the animal to antigenic material in a more sustained way (ibid: 94). The animal is more likely to mount a prolonged immune response with a good immunological memory (ibid: 94). Live organisms also provide an adjuvant effect that non-living delivery systems do not (ibid: 94).

Infectious Vectors

Immunocontraceptive vaccines can be delivered through genetically modified self-sustaining infectious vectors (Giovanna Massei & Cowan, 2014, p. 6). An ideal vector is species-specific, effectively transmitted between individuals, capable of carrying foreign DNA, and well-understood epidemiologically in the target population (Holt, 2003, p. 296). Although no vector has been used in the wild, several vectors have been developed in the laboratory for mice and rabbits (ibid: 296-297).

Once developed, vectors are likely to be humane, cost-effective, species-specific, large-scale, and long-term (Giovanna Massei & Cowan, 2014, p. 6). While the vector may need to be re-released, each release will have more impact because the vector may infect multiple animals or the same animal multiple times (Barlow, 2000, p. 899). An infectious vector may spread rapidly through the population and be transmissible even at low densities (Holt, 2003, p. 295). The vector will also self-regulate depending on the density of the target species (Jewgenow, 2017, p. 265). Some vectors, such as bacteria and viruses, are themselves immunogenic, which could enhance the immune response (Barlow, 2000, p. 899). Since the vector does not require human intervention to treat each individual, it is likely to be relatively inexpensive (Holt, 2003, p. 294).

However, the vectors are also irreversible and difficult to control once released (Giovanna Massei & Cowan, 2014, p. 6). The vector may mutate to affect non-target species, or the target species may evolve resistance (ibid: 6). Vectors may not have a sufficiently high transmission rate, may be inferior competitors with field strains, or may not induce infertility in the presence of field strains (Jewgenow, 2017, p. 271). Vectors may spread into populations we don't wish to contracept (ibid: 271). Quarantine may be required at ports to prevent transmission into populations whose size we don't desire to reduce (Williams, 2008). Immunocontraception by virus requires a very high dose of the virus which may be difficult to replicate under natural conditions (McLeod et al., 2008, p. 560). Many members of the public are suspicious of genetically modified organisms and thus likely to oppose their use (Holt, 2003, pp. 299–300).

Certain vectors may harm the animal's welfare. For example, myxomatosis, a rabbit disease that has been proposed as an immunocontraceptive vector, causes subcutaneous swelling and conjunctivitis that can lead to blindness (McLeod et al., 2008, p. 557). Salmonella and canine herpesvirus have been proposed as vectors for control of the red fox: salmonella infection can cause gastroenteritis and septicemia, while canine herpesvirus is fatal to neonates (ibid: 558). Macropod herpesvirus has been considered for use in brushtail possums: it causes eye and nasal discharge, lingual ulcers, and occasionally death (ibid: 559).

Miscellaneous

Immunocontraceptive vaccines may be delivered through a nasal route (Jewgenow, 2017, p. 270). Transcutaneous delivery of vaccines has also been explored (Brookhouse, Bucher, Rose, Kerr, & Gudge, 2013, p. 18).

In species that live, nest, or sleep underground, it may be possible to deliver an aerosol version of an immunocontraceptive vaccine directly into their holes (Tuyttens & Macdonald, 1998a, p. 352).

Conclusions and Directions for Further Research and Advocacy

I believe that wildlife contraception as the potential to be a cost-effective intervention to prevent wild-animal suffering.

This may seem like a premature conclusion: one thing I have emphasized throughout this paper is how little we know about wildlife contraception and how rarely it is used in the field. However, I believe wildlife contraception is promising, and its very neglectedness creates an opportunity for wild animal advocates.

Many proposals for reducing wild-animal suffering involve micromanaging many aspects of the animal's life, from providing supplemental food to curing or vaccinating against diseases to preventing infant mortality. Wildlife contraception takes the opposite approach. If animal populations are maintained below the carrying capacity, each individual animal enjoys more resources than they need. Food is abundant. Diseases and parasites more rarely reach the threshold density to maintain their presence in the population. No animal is left without a territory.

I am struck by the increased lifespans associated with wildlife contraception. While it has been rarely studied, the effects are remarkable. In wild horses, a new age class had to be invented, because mares were living to an age that no horse had ever lived to before. Surgical sterilization also improves lifespans for rabbits and adult female brushtail possums. Theoretically, in many species decreased populations due to wildlife contraception should result in a compensatory reproductive response: just as deaths increase, births decrease, or emigration increases when populations are above the carrying capacity, sometimes deaths decrease, births increase, or immigration increases when the population is below it. While birth rates and net migration are not relevant to wild-animal welfare, death rate is.

There are some serious welfare costs to wildlife contraception. Some forms of contraception eliminate the animal's libido, which means they don't have the pleasurable experience of having sex. All forms of contraception mean that the animal cannot experience parenting. Contraceptive delivery may result in some relatively minor harms, ranging from the stress of capture to abscesses and granulomas from remote delivery. PZP comes from factory-farmed pigs, thus contributing to farmed animal suffering. The effects of wildlife contraception on other species and ecosystems as a whole, particularly when the contraception isn't used on an overabundant species, is unknown.

Wildlife contraception is significantly under-researched. There are no effective and humane bird contraceptives. We don't know the effects of contraception on many mammal taxa, particularly those not typically kept in zoos. In the field, contraceptives have been used mostly on large mammals, particularly ungulates. Psychosocial effects have generally not been studied except when convenient to the investigators as part of a study on a different subject. Since the field has received so little funding, it is likely that better contraceptives and delivery mechanisms could be developed.

Wildlife contraception is very popular among the general public. However, there are no interest groups advocating for its adoption, while several well-organized interest groups such as hunters advocate against it. Naturally, this means wildlife managers are reluctant to use contraception, sometimes to the point of sabotaging studies. When there is a well-organized group advocating against the lethal control of certain animals, such as wild horses, contraception is far more likely to be used to manage the animals.

If wildlife contraception is more widely used, it is likely to become cheaper. Economies of scale will occur. Development of more effective and humane contraceptives will be incentivized, and delivery techniques will be honed and refined. We will also develop a larger body of knowledge about the effects of contraceptives on various species, allowing us to decide which species to use contraception on more knowledgeably. Discussion of wildlife contraception will allow us to spread the norm of caring about wild animals, which will make future interventions easier.

One approach is to advocate for the control of overabundant animals with wildlife contraception. A second, complementary approach is to develop and market contraceptives individuals can use, such as ContraPest. Not only will this prevent the use of inhumane traps and poisons, but it will target rats, mice, and other short-lived and fast-breeding species which are particularly likely to have poor welfare. Individually marketed contraceptives can also be used more easily to reduce populations by people concerned about wild-animal suffering, without having to go through a government bureaucracy. (I imagine a birdseed with contraceptives marketed towards people concerned about wild-animal suffering.)

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