Contraception in wild animals

A REVIEW OF ITS USE IN MAMMALS

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Animal Ethics

Published in 2023 by Animal Ethics

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Suggested citation: Gutiérrez, J. & de Miguel, F. J. (2023) *Contraception in wild animals: A review of its use in mammals*, Oakland: Animal Ethics, retrieved from https://www.animal-ethics.org/contraception-wild-animals-mammals.

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Abstract

Properly planned use of contraceptive methods in wild populations of various mammalian species can be successfully used to prevent lethal methods from being implemented, especially in urban and suburban areas. This study aims to review the most significant literature to date in relation to contraceptives. We have reviewed the modalities of application of immunocontraceptive vaccines, the evidence about the effectiveness of immunocontraception, the physiological, reproductive, ethological and social effects on the animals involved; and what the public's reaction to immunocontraception will be. The available evidence indicates that significant detrimental side-effects are unlikely, both for the animals targeted by these programs and for other animals and humans, although more studies would be useful to confirm this.

Introduction

Interventions to limit the size of certain animal populations are usually motivated by human interests. These aim to avoid various situations where the presence of animals is in conflict with human populations, for reasons that include the transmission of infectious diseases (e.g. Spielman et al. 1985; Kilpatrick et al. 2014; Stein 2011), the impacts on animals of vehicles and airplanes (Conover et al. 1995), or the impact of animals on crops, among others (Conover & Chasko 1985; Fairaizl 1992; Curtis & Decker 1993; Ettl 1993; Barlow 1996; Fagerstone et al. 2006; Smith & Wilkinson 2003; Wilson 2005; Sterner & Smith 2006; Massei et al. 2011). Nevertheless, increases in populations in a certain space could also be quite harmful to the animals themselves. In particular, increased populations could cause famines and nutritional deficiencies (Martínez M. & Hewitt 2001), as well as facilitate the transmission of diseases.

In general, when populations are so large that they exceed carrying capacity, the welfare of the animals tends to decrease (Jewell & Holt 1982). Populations with fewer members than their carrying capacity are usually made up of individuals of greater size and weight and superior health (Jewell 1982). On the other hand, populations that exceed their carrying capacity tend to have individuals with reduced size, deficient physical condition, high parasitic load, and a high prevalence and contagion of infectious diseases (Killian et al. 2006a), as has been reported for deer (Coulson 1999; Slate et al. 2000). Therefore, a manageable strategy for reducing the suffering of wild animals could be to keep populations below their natural carrying capacity (Brennan 2018).

Additionally, the possibility of keeping animal populations from increasing beyond a certain limit could be key for making other kinds of actions to help them possible. For example, combined with programs for vaccination against certain diseases, it could prevent negative effects of diseases without causing a significant increase in the size of the vaccinated populations. Otherwise, the size of the vaccinated population would tend to increase because of a reduction in disease-induced death rates and reproductive problems.

The most common response in the face of population growth of certain animals has consisted of lethal practices such as hunting, trapping, or poisoning (Curtis et al. 2002). These methods are becoming more and more restricted, and often they are not feasible in regional parks or suburban areas where many animals regularly approach human population centers.

Furthermore, growing swaths of society are opposed to lethal population control for moral reasons motivated by a consideration for animals, and they demand fertility control measures, or other non-lethal methods, from their respective governments as tools for population management (Kirkpatrick 2002). Despite public pressure, the development and use of fertility control techniques has been slowed down as a consequence of the difficulty in developing effective and feasible contraceptive methods (Fagerstone et al. 2006).

Fertility control methods include any reproduction inhibition method, such as hormonal contraception, surgical and non-surgical sterilization, intrauterine devices, and immunocontraception (Brennan 2018). Among the variety of contraceptive methods currently available are chemical methods (synthetic hormones), immunocontraceptive vaccines, and other contraceptives. In addition to these methods, there are other non-contraceptive population management strategies, such as the translocation of individuals.

Translocation can be stressful for the animals involved, but it can also be useful depending on the species and what threats they face. For instance, long-distance translocation of bears has reduced both human-caused mortality (not surprising) and natural mortality (Bauder et al. 2021). Nonetheless, translocation can increase mortality in the transported animals as well as in animals belonging to the receiving population, and it is relatively expensive, and has the potential to spread diseases and pathogens (Daszak et al. 2000; Fischer & Lindenmayer 2000; Massei et al. 2010b). Fischer & Lindenmayer (2000) reviewed more than 180 studies on animal relocations (reintroductions, translocations, etc.) and found that translocations with the objective to resolve conflicts between humans and animals generally failed.

Surgical contraceptive procedures are difficult to use in wild animal populations consisting of many individuals, although they have been used on occasion, for example, in populations of white-tailed deer (*Odocoileus virginianus*) (MacLean et al. 2006; Patton et al. 2007). In addition to being irreversible, surgical sterilization is more expensive and invasive, requires guaranteeing the correct postoperative care in a veterinary center, and contributes to the risk of infection (bacterial and parasitic) and hemorrhage in the individual (Amatayakul-Chantler et al. 2013). Furthermore, these types of procedures have a time restriction, since they generally must be performed during the animal's prepubescent stage in order to reduce stress, which at the same time prevents the animals from attaining optimal prepubescent development (Machado et al. 2016).

Contraceptive methods must always be adapted to the physiology of the particular animal, and there are no contraceptive agents that are equally effective and appropriate for use in all species (Kirkpatrick 2002), nor in all age ranges. For example, in contrast to what has been demonstrated for adults, in three-month-old fawns, immunocontraceptive vaccination using GnRH (GonaCon™) vaccines did not induce a lasting immunocontraceptive response, nor did it affect the sexual development of the individuals (Miller et al. 2008).

Contraceptive techniques also should not cause significant side effects that potentially compromise the treated individuals' physiology or development (Quy et al. 2014). This is not to say that they must not present any mild side effects, rather that there should be no harmful effects that threaten the animal's welfare. For example, females whose reproduction is temporarily or permanently inhibited will have, as a general rule, fewer energetic requirements and, therefore, will be less active than females that are caring for their offspring (Quy et al. 2014). While these changes are not considered serious, if the fertility control method causes a notable impact in the behavior of individuals (e.g., an increase in aggressive behaviors), its use could be considered problematic from the perspective of animal welfare. Nevertheless, it would still be preferable to the deaths of these animals. Moreover, such side effects could be considerably less harmful than what the animals might otherwise suffer if, for example, they were subject to famine or nutritional deficiency.

After extensively reviewing the contraceptive treatments for wild species, little scientific evidence was found regarding alterations in the movement and activity of the animals who were treated (Gray & Cameron 2010), with reviewed studies including species such as eastern gay kangaroo (*Macropus giganteus*) (Woodward et al. 2006), common brushtail possum (*Trichosurus vulpecula*) (Ramsey 2007), and red fox (*Vulpes vulpes*) (Saunders et al. 2002), among others. For example, in wild boar (*Sus scrofa*) females treated with contraceptives, no alterations were found in body weight, hematology, biochemistry, or social rank, in comparison to the females of the control group (Massei et al. 2012).

Contraceptives for mammals: immunocontraceptive vaccination

Immunocontraception consists of using an animal's immune system with the goal of producing antibodies that interfere with the activity of the proteins present in the gametes, reproductive hormones, and other proteins essential to reproduction (Talwar & Gaur 1987; Fagerstone et al. 2006; Kirkpatrick et al. 2011). That is to say, it consists of administering a vaccine made up of proteins that causes the production of antibodies. The antibodies that the animal generates interfere with the biological activity of reproductive proteins (Talwar & Gaur 1987) and, depending on the antigen and the formulation of the vaccine, the effectiveness can last for one to four years, or even more, whether delivered in single injections or multiple injections (Kirkpatrick et al. 1991; Miller et al. 1999; 2013).

The most common immunocontraceptive procedures are PZP (*Porcine Zona Pellucida*) vaccines, GnRH (*Gonadotropin Releasing Hormone*) vaccines, antisperm antibodies, and luteinizing hormone (LH) receptor vaccines. Since this review focuses on wild mammalian species, and LH vaccines are mainly used against fertility in dogs and cats (Saxena et al. 2002; 2003; Gupta et al. 2014), they have not been included in this study.

PZP vaccines

PZP is a glycoprotein formed by the combination of three proteins of the zona pellucida (ZP) extracted from pig (*Sus scrofa domesticus*) ovaries. The antibodies against ZP block the spermatozoa that penetrate the ZP layer and interfere with the maturation of the ovum (Dunbar & Schwoebel 1988). In other words, the PZP vaccine is only effective in females, and causes the animal's immune system to produce antibodies that interfere with the attachment of sperm to the ovum (Florman & Wassarman 1985).

PZP has been studied in a wide range of species, which confers robustness on the body of existing scientific literature. For example, PZP has generated inhibition of fertility in dogs (Mahi-Brown et al. 1985), baboons (Dunbar et al. 1989), donkeys (Turner et al. 1996), wild horses (Kirkpatrick et al. 1990; Garrott et al. 1992; Killian et al. 2004), and white-tailed deer (Miller & Killian 2000; Miller et al. 2001). On the other hand, it has not been effective in cats (Jewgenow et al. 2000) or rodents (Drell et al. 1984).

Nevertheless, PZP vaccines present some disadvantages. First of all, inoculation in the female twice in a period of four to six months is necessary, and with the accompanying administration of an adjuvant. Secondly, like other contraceptives, PZP vaccines do not largely affect mortality unless the mortality rates of the population are very high, so the effect of reduced fertility takes time to have an impact on the population density. Another disadvantage is that the PZP vaccine can produce multiple estrous cycles, as shown for female deer (Fagerstone et al. 2006, Ansari et al. 2017), which could result in late season births if antibody titers fall below a critical threshold.

GnRH vaccines

GnRH is a hormone that stimulates the release of gonadotropins from the pituitary gland, triggering a cascade of reproductive hormones (estrogen, progesterone, and testosterone) which leads to the production of sperm in males and to ovulation in females (Miller et al. 2013).

GnRH vaccines stimulate the production of antibodies that bind to the GnRH hormone, that is, antibodies against the individual's own GnRH (United States Department of Agriculture 2007). GnRH is a neuropeptide hormone that is naturally secreted from the neurons of the hypothalamus, and is responsible for the synthesis and release of two other hormones fundamental for proper reproductive physiology: LH (luteinizing hormone) and FSH (follicle-stimulating hormone) (Hazum & Conn 1988 in Baker et al. 2004). In particular, long-term treatment with GnRH agonists prevents ovulation and causes gonadal atrophy via (1) the decrease of GnRH receptors in the gonadotropic cells of the adenohypophysis, (2) reduction in the sensitivity of the GnRH receptor (Nett et al. 1975), (3) the decrease of pituitary LH content, and (4) the suppression of pulsatile secretion of LH and FSH (Aspden et al. 1996).

In order to achieve a contraceptive effect, these vaccines must be composed of numerous GnRH peptide molecules attached to a protein, thus forming what is known as a "conjugate," and their application in treated animals also requires an adjuvant (Miller et al. 2013). Upon binding to GnRH, the antibodies reduce the ability of GnRH to stimulate the release of these sex hormones. As a result, sexual activity decreases, and the animals remain in a non-reproductive state as long as there is a sufficient level of antibody activity (United States Department of Agriculture 2007).

In summary, immunization against GnRH causes the cessation of ovulation and follicular development in females (Patton et al. 2007) by reducing of the secretion of other reproductive hormones (Miller et al. 2004; 2008; Fagerstone et al. 2006). As is to be expected, the effects are not lifelong for the individual. To the contrary, after a decrease in antibody titers, natural reversal occurs in the majority of immunized animals (Keeling & Crighton 1984, in Patton et al. 2007).

GnRH is not species- or sex-specific. Thus, in contrast to PZP-type vaccines, anti-GnRH vaccines can be used in males as well as females. The contraceptive effects of a single-injection vaccine last from one to two years without a booster and are reversible with time as antibody levels decrease, although multiple injections can cause permanent sterility (Molenaar et al. 1993).

Beyond the expected change in sexual and reproductive behavior, large changes in the behavior or social organization of most species are not expected, besideswhich vaccine protein antigens are broken down into amino acids in the gastrointestinal tract, so no component of the vaccine enters the food chain (Miller et al. 2013), and it does not enter muscle tissue (Fagerstone et al. 2006; Miller et al. 2013). Additionally, this vaccine has not interfered with the ability to get pregnant in deer (Miller et al. 2008), elk (*Cervus canadensis*), American bison (*Bisonbison* sp.), and wild horses (*Equus caballus*) in subsequent years (Miller et al. 2004; Killian et al. 2008; Powers et al. 2012).

Mammalian GnRH is expected to be effective in reducing fertility in the majority of mammals, including rodents. In fact, GnRH vaccines have already been utilized as immunocontraceptive agents in dogs (Ladd et al. 1994), cows (Robertson et al. 1982), horses (Rabb et al. 1990), sheep (Schanbacher 1982), pigs (Meloen et al. 1994), and black rat (Massei et al. 2020).

The contraceptive efficacy of these vaccines is very high. For example, single-dose anti-GnRH vaccines were effective in reducing the size of a population for a period of up to 36 weeks when wild boar femaleswere given the vaccine(Killian et al. 2003) although an inferior response to the vaccine was obtained when maleswere treated (Killian et al. 2009). In a seven-year study carried out by Miller et al. (2000), in which white-tailed deer were vaccinated once a year for just the first two years, there was an 88% reduction in offspring in the first two years, and 74% during the total of the first five years.

These vaccines have been commercialized for years under the name GonaCon™, and their use as a tool for fertility control in species like deer has been extended (Fagerstone et al. 2006). In fact, in female deer, a single injection of GonaCon™ has achieved infertility for two to four consecutive years (United States Department of Agriculture 2007), with an efficacy of 80-100% (Killian et al. 2008b), and always more than one year in any case (Hobbs et al. 2000), without requiring a second dose. In particular, GonaCon™ is able to considerably reduce associated reproductive behaviors for at least two years (Killian et al. 2008b), including heat cycles, and so can serve as a tool to control the transmission of venereal diseases and diseases transmitted during birth (Miller et al. 2013).

In contrast, white-tailed deer females treated with PZP had a prolonged reproductive season and repeatedly returned to estrus. A year after being vaccinated, females vaccinated with PZP had more observed estruses than females treated with GnRH (Curtis et al. 2002). In another study carried out by Killian and Miller (2000), the females treated with PZP continued reproducing for an average of 150 days, while the average for the females of the control group was 45 days, similar to that of the females in the GnRH group. In this same study, it was observed that the males immunized with GnRH did not have interest in sexual activity when they paired up with females of the control group (Killian & Miller 2000). These findings seem to tip the scales in favor of GnRH vaccines rather than PZP vaccines as fertility control methods.

Immunocontraception via antibodies for GnRH is already being developed using baits containing these contraceptives for species where population control is relevant, such as wild boars (Massei et al. 2010a). This way, the whole process of immobilization, capture, and vaccination would be avoided. Nevertheless, before oral contraceptives can be used as effective tools in wild animal population management, studies testing the adequate dosage and frequency for each species are needed, as well as optimization in the formulation of the bait and in the feasibility and costs of the method (Massei et al. 2020). The current challenges that science faces in the development of oral vaccines have recently been reviewed by Vela Ramirez et al. (2017).

Modalities of application

Remote delivery of vaccines

Remote immunocontraception delivery systems are directed at individual animals, which allows for adapting dosage according to body weight. These systems include bio-bullets (biodegradable projectiles) and darts (Massei & Cowan 2014), and can be used to deliver vaccines, steroid hormones, or GnRH agonists (Asa & Porton 2005).

Even though both capture and remote delivery could cause stress in the animal (Jewgenow 2017), remote delivery systems generally minimize the stress (Hampton 2017) and can avoid the cost and labor involved in capture (Massei & Cowan 2014).

However, these systems present a few other limitations. For example, some individuals could be vaccinated several times by error, or the injection might miss the muscle partially or totally (Asa & Porton 2005; Gupta et al. 2011). While the majority of contraceptives are innocuous when administered several times, multiple administrations of progestogens can produce side effects such as immunosuppression (Gupta et al. 2011).

Over time, remote delivery of vaccines loses effectiveness (Jewgenow 2016). The animals become more wary, and vaccination not only slows down, but also becomes more expensive, because the untreated animals are the most cautious about letting themselves be seen, as has been reported in deer (living in Irondequoit, New York, US) (Rudolph et al. 2000). Another limitation for remote delivery of vaccines could be population density. When the animals have a low population density, delivery gets more expensive, and some areas could be inaccessible for this type of implementation, due to opposition from landowners, vegetation, and proximity to roads and urban areas (Rudolph et al. 2000).

Remote delivery of contraceptives in deer and wild horses has been implemented on occasion, following the horses on foot and shooting them with darts or placing bait in food or water. However, state agencies in charge of wildlife management often require individual tagging of treated animals, so the contraceptive is administered manually (Gupta et al. 2011; Turner & Rutberg 2013). Occasionally, tagging can cause pain and behavioral alterations in animals, as has been reported for swimming, maternity, and feeding behaviors in marine mammals (Walker et al. 2012).

For other animal species, techniques have become more refined and expensive. For example, since elephants tend to avoid vehicles that approach them, contraception delivery from helicopters emerged as a good option, since elephants' ability to flee is less effective than it is with land vehicles. Even so, the use of helicopters is potentially dangerous due to the need to fly at low altitude, and it causes stress in the animals (Delsink et al. 2007).

Remote delivery of vaccines may cause more cases of abscess, due to dirt present on the skin surface entering into the injection site. However, these abscesses generally drain in two weeks without negative consequences for the individual's health in the long-term (Kirkpatrick et al. 2009).

Oral vaccines

Orally administered immunocontraceptive vaccines involve the use of bait, whether it be food or water. The expectation is that the animals will be attracted to the bait without difficulty, and, in fact, the PZP-type vaccine in genetically modified carrots has had success in controlling fertility in possums (Barlow 2000). However, this kind of implementation still presents several challenges. First of all, the oral method does not ensure that each individual will receive the same dose (Asa & Porton 2005). It is likely that individuals of lower social status will be largely excluded from the bait, not consume a sufficient quantity, and, therefore, not receive a complete dose (Brennan 2018).

Secondly, the immunocontraceptive might not be distributed in an even manner throughout the food, or the animals might refuse to eat food with an unusual taste or appearance. Even if it is ingested without difficulty, the immune system has a relatively high threshold for recognizing an orally administered antigen as “foreign” and activating a cascade of defense mechanisms (Massei & Cowan 2014). This could mean that orally administered immunocontraceptive vaccines need to be administered repeatedly over time.

Thirdly, the bait and its method of distribution must be chosen correctly in order to be attractive enough to the target species of the treatment and have a population effect without attracting other species (Asa & Porton 2005; Massei & Cowan 2014).

Vaccines implemented via viruses and bacteria

Contraceptive vaccines administered via viruses or bacteria use these organisms as genetically modified infectious vectors (Massei & Cowan 2014). The administration of immunocontraceptive vaccines via viruses and bacteria uses a relatively simple method: the gene for a specific vaccine (for example, PZP) is inserted into the genetic material of a non-pathogenic virus, and this, in turn, is introduced into the specific animal population, thus affecting the infected animals and achieving, as a result, contraception (Kirkpatrick 1999).

Currently, researchers have also used virus-like particles, such as lipoprotein nanoparticles, that do not replicate but that resemble viruses immunologically (Cross et al. 2011). Unfortunately, there still is not any data available for animals relevant to population management such as ungulates, although studies are also underway to address this gap (Cowan & Massei 2008; Cross et al. 2011).

The implementation of immunocontraceptive vaccines via viruses or bacteria does not require human intervention and can be developed with specificity for species, or at least for family (e.g., canids, felids, etc.), facilitating the prolonged immune response process with an effective immunological memory (Kirkpatrick 1999). Besides, some vectors, like bacteria and viruses, are themselves immunogenic, which could enhance the immune response (Barlow 2000).

However, implementation via infection presents a series of challenges. Firstly, these are irreversible vectors that pose the risk of getting out of control once released and mutating quickly and infecting other species, including humans (Kirkpatrick 1999; Barlow 2000; Massei & Cowan 2014).

Secondly, the target species could develop resistance, and the vectors might not have a sufficiently high transmission rate, could be inferior competitors to field strains, or might not induce infertility in the presence of field strains (Jewgenow 2016).

Thirdly, certain vectors could harm animal welfare. This would be the case of myxomatosis, a disease in rabbits that was proposed as an immunocontraceptive vector for this species. However, it causes subcutaneous inflammation and conjunctivitis that can lead to blindness (McLeod et al. 2007).

Finally, the possibility of using genetically recombinant proteins or genetically modified viruses for the development of vaccines for reproductive inhibition could be unacceptable to some people (Brennan 2018). The most recent advances have moved on from using bacteria or viruses as vectors for inducing immunocontraception to the use of plants, especially for contraception in animals with herbivorous diets. For example, female possums (*Didelphis virginiana*) vaccinated using bait made from edible vegetal material that included immunocontraceptive antigens expressed in potatoes (*Solanum tuberosum*) showed reduced fertility and an immune response to the antigen (Jewgenow et al. 2000). More studies are still needed for the development of a "*plant-based*" immunocontraception (Polkinghorne et al. 2005).

Effectiveness of immunocontraception

In general terms, any fertility control method using contraception is considered effective and reversible when no offspring are born while the contraceptive is in use, but are born when the contraceptive is no longer in use (Asa & Porton 2005).

The current methodology available for carrying out non-lethal fertility control in wild populations has recently been reviewed (Fagerstone et al. 2010; Kirkpatrick et al. 2011; McLaughlin & Aitken 2011; Massei & Cowan 2014). Basically, contraceptive methods must guarantee the following: (1) no effects, or acceptable effects, in the physiology, welfare, and behavior of the animals; (2) high effectiveness with the administration of a single dose; (3) infertility for the majority of the treated animals during their potential reproductive lifespan; (4) inhibition of female reproduction, or ideally the reproduction of both sexes; (5) no effects on lactation or pregnancy; (6) relatively low costs of production and implementation; (7) total inability to enter the food chain; (8) possibility for remote delivery; (9) species specificity; (10) stability in a wide range of field conditions; (Massei & Cowan 2014); (11) able to be implemented on a large scale; (12) ethical acceptability; and (13) having as its aim reducing the birth rate and not increasing the mortality rate (Machado et al. 2016).

To know whether fertility control is biologically feasible or financially favorable compared to other control methods for a particular species, several specific factors must be taken into account, e.g., population figures, proportion of the sexes, age structure of the population, whether it is an open or closed population, estimated growth and mortality rates, etc. (Curtis & Decker 1993; Nielsen et al. 1997; Fagerstone et al. 2006). For example, in free-ranging populations, a contraceptive method is considered effective if 50-60% of treated animals are sterile (Asa & Porton 2005).

Using the estimate of the adult survival rate and the age at which animals reproduce, it is possible to quantify the percentage decrease in population size in relation to the number of animals sterilized in comparison with lethal control measures, in order to compare the relative effectiveness between both techniques for a given population (Dolbeer 1998). Results from Dolbeer demonstrate that, for those species in which females reproduce in their first year of life and few few animals survive to adulthood survive, fertility control could be an efficient management tool. That is to say, fertility control seems to be more effective in species of small size with high rates of reproduction and low rates of survival, such as rats (*Rattus* spp.), than in large species with lower rates of reproduction and high rates of survival, such as deer. However, many rodent species breed all year long, so oral contraceptives must be administered with food periodically in order to reduce reproduction rates. Species that are seasonal breeders, like prairie dogs (*Cynomys* sp.) and ground squirrels (*Spermophilus citellus*), could be good candidates for an effective use of contraceptives (Yoder et al. 2016).

Even though fertility control techniques that inhibit reproduction for only one year have been shown not to be effective in rapidly reducing population density in species like deer, they could serve as an effective tool for stabilizing population growth in these species of large size (Nielsen et al. 1997). Specifically, the proportion of treated deer would depend on the average reproduction rates and the age distribution of the females of that population (Fagerstone et al. 2006).

The recent development of contraceptives has achieved an immune response of two to five years (Madridejos 2017), although some studies say up to six years (Killian et al. 2008b). In other words, the effects of a single vaccination would last several years, making population management using fertility control more feasible every day(Fagerstone et al. 2006).

Effects of immunocontraception on the health of animals

Neither the PZP vaccines (Kirkpatrick et al. 2009; Fagerstone et al. 2010) nor the GnRH vaccines (Fagerstone et al. 2010) have shown significant harmful effects in the health of treated animals. No negative health consequences have been reported from accidentally administering multiple doses of the GnRH vaccine to an animal (Miller et al. 2013). In general, the blood parameters of treated animals seem to be in the normal range for their species (Kirkpatrick et al. 2009).

More specifically, GnRH vaccines do not affect the size of lymph nodes, body temperature in cows (Massei et al. 2015), blood parameters in white-tailed deer (Gionfriddo et al. 2011), biochemical or hematological parameters in wild boars (Massei et al. 2012), or hepatic and renal function and nutritional state in prairie dogs (*Cynomys* spp.) (Yoder & Miller 2010).

Physiological effects

The most common and visible short-term effects of immunocontraceptive vaccination are the possible reactions at the injection site (Brennan 2018). PZP vaccines rarely cause reactions at the site of injection, although granulomas are more frequent with this type of vaccine (Massei & Cowan 2014). For example, these granulomas have been reported in elephants, although the vast majority of them were reabsorbed (Delsink et al. 2007).

In deer, granulomas were found at the injection sites of most individuals, even two years after the treatment (Curtis et al. 2007), while other studies concluded that only 0.5% of vaccinated individuals experienced an abscess as a consequence of the vaccine injection (Kirkpatrick et al. 2009). For example, in fox squirrels vaccinated with GnRH, 87% of the animals had an abscess as a consequence of the injection (Krause et al. 2014).

GnRH vaccines caused reactions in the lymph nodes of white-tailed deer, which can cause secondary granulomatous inflammation and hyperplasia (Gionfriddo et al. 2011). In a study of deer treated with GnRH (GonaCon™), no adverse health effects related to vaccination with GonaCon were detected, except for localized intramuscular reactions in the injection site in 29% of individuals (5 of 17 females), including chronic abscesses in four of them and a granulomatous nodule 2 years after injection (Gionfriddo et al. 2009), which highlights the importance of long-term follow-up. Only one of the females developed serious local lesions with signs of infection (Gionfriddo et al. 2009).

No evidence of limping, difficulty moving, or injuries that are visible or detectable through veterinary palpation have been reported in animals suffering from the granulomas that the GnRH can cause in deer (Massei & Cowan 2014). and in moose (Ransom et al. 2014). However, deer with a poor general health condition or with a high parasitic load may have higher chances of experiencing a reaction at the vaccine injection site (Miller et al. 2013). In fact, in white-tailed deer, reactions to the GnRH vaccine may be less common in captive animals than in wild animals (Miller et al. 2013).

Regarding general body condition, some recent studies show that the PZP vaccine improves the body condition of treated animals (e.g. Kirkpatrick et al. 2009), although other studies (even on the same species) concluded that PZP has no effect on body condition (Gray & Cameron 2010). In a study of deer treated with PZP, general body condition was between good and excellent (Curtis et al. 2007). GnRH vaccines generally don't affect body condition (Gray & Cameron 2010). This has been reported for horses (Ransom et al. 2014), cows (Massei et al. 2015), prairie dogs (Yoder & Miller 2010), and white-tailed deer (Gionfriddo et al. 2011). In the case of white-tailed deer, it seems that the improvement in body condition could be related to the fact that females do not go into heat, nor do they become pregnant (Gionfriddo et al. 2011). Vaccination with GnRH has also demonstrated improvement in body condition in the wild boar short-term (Massei et al. 2008), but not long-term (Massei et al. 2012). However, fox squirrels vaccinated with GnRH vaccines had a worse body condition, which could be due to the high rate of abscesses (Krause et al. 2014).

Effects in the reproductive system

PZP vaccines change the number, weight, and size of ovarian follicles and can cause the loss of ovarian function, oophoritis (inflammation of the ovary), and cyst formation (Gray & Cameron 2010). Ovary damage has not been detected in primates, horses, or deer, but has been found in dogs, rabbits, mice, sheep, and some primates (Kirkpatrick et al. 2009; 2011).

In deer, PZP can cause eosinophilic oophoritis (the accumulation of a certain type of white blood cell in the ovary, which causes inflammation) and reduction of the number of normal secondary follicles (Lauber et al. 2007). Some studies debate whether purified ZP proteins lower the risk of ovary problems related to the ZP vaccines in deer (Massei & Cowan 2014).

Additionally, GnRH-type vaccines change the number, weight, and size of the ovarian follicles (Gray & Cameron 2010). While there are no effects reported on the rest of the organs of deer treated with GonaCon™, the reproductive organs do experience effects upon treatment. The sizes of the mammary glands, uterus, and ovaries are reduced (Gionfriddo et al. 2009).

Ethological and social effects

The effects of immunocontraception on the reproductive physiology of animals can alter their natural behavior, and this can affect their ability to solve problems in their environment (Hampton 2017). However, the majority of studies conclude that the changes in behavior of animals treated with immunocontraceptive vaccines do not have a significant impact on animal welfare (Gray & Cameron 2010). In fact, Hampton (2017) affirms that the contraceptive techniques not resulting in an alteration in the normal hormonal equilibrium of the animal may allow for more normal behavior than contraception through endocrine suppression, and, as a result, greater welfare.

In social animals, immunocontraception may modify behavior patterns and social interactions, and thus have an impact on group structure. Even though theoretically we might expect infertility to lead to the loss of pair bonds (Asa & Porton 2005), to date, not enough studies have been conducted to allow generalizing the conclusions on the effects of immunocontraception on social behaviors and welfare, and the ethological observations of the different studies have normally been of short duration (Gray & Cameron 2010). One recent study has reported that time spent together with peers or mates can increase, decrease, or not vary as a result of contraception, depending on the treated species (Ransom et al. 2014). For example, in studies on canids, pair bonds seem to persist in spite of the contraceptive (Asa & Porton 2005). Treatment with GonaCon™ in horses reduced behaviors of fidelity to the family group (Ransom et al. 2014).

On the whole, caring for offspring is an elemental and complex natural behavior in many animal species (Hampton 2017). Consequently, the absence of offspring could negatively affect the welfare of females as well as that of the group (Asa & Porton 2005). Another point already discussed by previous authors is the possibility of whether depriving animals of fertility could lead to depriving them of a rewarding experience or the opportunity to satisfy their preferences (Hampton 2017).

For example, contraception in elephants can precipitate a reduction in family group cohesion, which gives rise to larger herds and altered social structures (Kerley & Shrader 2007). Often, elephants use allomaternal care with their young, essential for first-time mothers to learn how to care for their offspring. If fertility control using contraception affects social structure, the mortality rate of the females' first offspring may increase. Reducing the number of offspring and the size of the group could increase the frequency of attack behaviors toward the young. This can increase the stress, and affect milk production of their mothers (Kerley & Shrader 2007). This aspect should be considered carefully for any contraception planning in highly social animal species.

To date, the literature on evidence for individual behavior modification is not conclusive. The effects of contraception on aggression are not well understood (Asa & Porton 2005), and studies show that contraception may increase, decrease, or have no effect on aggressive behaviors (Ransom et al. 2014). Aggressive behaviors are difficult to evaluate, since they depend on external factors, like competition, season, age, species, demographics, dosage, and treatment duration (Asa & Porton 2005).

Regarding the behavior of moving and traveling within the habitat, it is to be expected that vaccinated females exhibit less travel than untreated females, since the latter would generally become pregnant and would travel in search of food, shelter, and other resources. Nevertheless, the majority of studies find a minimal impact on distribution area and movement patterns in treated animals (Gray & Cameron 2010; Quy et al. 2014).

Public opinion regarding immunocontraception

Using immunocontraceptives for fertility control is unpopular in some circles (Warren 1995; Fagerstone et al. 2010). It is often thought that lethal methods should continue to be used on animals going forward. Also, some conservation organizations tend to minimize or ignore the ethical implications of the actions they promote and that entail harm to individual animals, as occurs in the case of their being hunted (Ramp & Bekoff 2015; Kareiva et al. 2017; Wallach et al. 2018). A growing body of scientific evidence should push these organizations to reconsider their lack of concern for the welfare of individuals (Sekar & Shiller 2020).

Nevertheless, there is a clear growing trend focused on the search for methods other than hunting (Fagerstone et al. 2006). Owing to clear social preference, many agencies in charge of wild animal population management are opting to fund the reproductive control of wild animal populations (Fagerstone et al. 2006; Dunn et al. 2018).

Due to the fact that traditional practices such as hunting, trapping, poisoning, or the introduction of predators bring about suffering and death for animals (Sharp & Saunders 2011), reversible contraception could be a suitable tool for the control of animal populations. Nevertheless, it is a relatively modern technique that should be developed more to increase its effectiveness.

In line with what was mentioned before, as a general rule, those who were surveyed regarding contraception and who were interested in maximizing opportunities for deer hunting and reducing financial costs were opposed to contraception (Curtis & Decker 1993). Those who defend contraception for wild animals include: (1) scientists who are intellectually interested in contraceptives for wild animals, (2) people who work in environmental management, including public health authorities concerned with the consequences of increases in wild animal populations, (3) animal advocates opposed to methods that involve the death of animals, and (4) political groups interested in supporting the positioning of a sector of the population in favor of non-lethal control methods.

The opponents of these techniques include: (1) hunters who believe that fertility techniques will replace hunting as a population control method, (2) state agencies that are financially dependent on hunters, and (3) a few animal organizations who think that contraception is unethical because it interferes with animals' control over their own reproductive life (Asa & Porton 2005).

There are other arguments against immunocontraception in general terms that still deserve to be evaluated and studied scientifically. For example, in studies in which dominant males are the objects of sterilization, the majority of females will be impregnated by males who would not have been the primary breeders or that the females would not have originally preferred, which could cause serious genetic consequences (Asa & Porton 2005). On the other hand, if only certain females reproduce, there could be the risk of inbreeding in future generations (Jewgenow 2016). In addition, if the population of a prey species is reduced as a consequence of the fertility control of its individuals, it is likely that predators will go on to hunt a different prey species (Jewgenow 2016).

Nevertheless, both supporters and opponents of contraceptive animal control appear to be in agreement that any animal control policy should be based on science, involve various interested groups, and, ultimately, be effective (Lauber et al. 2007).

Discussion and future perspectives

Immunocontraception allows for long-term efficacy in the maintenance and reduction of wild animal populations (Hampton et al. 2015) and is put forward in the present day as an alternative to lethal control, especially in urban and suburban environments.

The contraceptive treatments being used are not showing notable side effects in treated individuals. Nevertheless, several authors have expressed the need to increase scientific studies of the effects of contraceptive vaccines on the physiology and behavior of wild animals (Quy et al. 2014), for example, through longitudinal studies that include various bioindicators of animal welfare (e.g. physiological, demographic, and ethological).

In fact, most studies are short-term and only deal with health issues, without considering and debating the effects of contraception on the affective states of the animals, experience of the environment, nutrition, and ability to perform natural behaviors (Hampton 2017).

Immunocontraception could compromise animal welfare during capture, immobilization, handling, and administration of the treatment, potentially causing stress, and could influence the individual's natural behavior by depriving them of biological functions such as reproduction and caring for offspring (Hampton et al. 2015). However, to date, most scientific studies on fertility control methods have focused on their efficacy, and few have conducted an extensive evaluation of animal welfare (Hampton et al. 2015).

The consequences for individual welfare, both short- and long-term, should be considered and rigorously evaluated, and the selection of methods that entail less impact on animal welfare are preferable. For example, the development of remote delivery systems, such as progestin implants (Kirkpatrick et al. 1990) and GnRH agonists (Baker et al. 2005), reduce the short-term welfare risks associated with treatment administration (Hampton et al. 2015).

In addition to the lack of studies regarding individual welfare, contraception for wild animals is scarcely studied in many taxa of mammals, especially in those not normally found in zoos (Brennan 2018). A great deal of the research on contraceptives for animals focuses on the orders Perissodactyla (especially horses), Artiodactyla (especially deer and domesticated cows), and Carnivora (especially felines) (Gray & Cameron 2010). In the field, contraceptives have been utilized and evaluated mainly in large mammals, ungulates in particular, but studies in other species have not easily obtained funding. The data continue to be quite scarce for mammals other than carnivores, ungulates, and primates (Asa & Porton 2005), so more studies are needed which are more extensive and are carried out on other wild animal taxa.

At the same time, the development of vaccines that come from bacterial cultures or in *plant-based*(e.g. Jewgenow et al. 2000; Polkinghorne et al. 2005) baits could present an alternative that prevents animal suffering in fertility control.

Of all the methods of endocrine suppression in animals developed to date, it is likely that immunocontraception with GnRH is the one that least compromises animal welfare (Hampton et al. 2015). Immunocontraception using GnRH antagonists induces the partial suppression of hypothalamic-pituitary-gonadal axis function (Powers et al. 2011), but the effects are not as profound as those of gonadectomy (Hampton et al. 2015), and it has advantages when compared to PZP vaccines.

Other limitations of contraception for wild species are that it does not always allow for the reduction of the number of individuals of a population in a short time and that it is more expensive than traditional methods. In populations of animals with short lifespans such as rodents, contraceptives can quickly reduce population density, but in populations of long-lived species, such as deer, contraceptives do not allow for an immediate reduction in the number of individuals, so if they are causing any harm to human activity, that harm will remain (Fagerstone et al. 2006).

If contraception for wild animals were more widely used, development of the more effective contraceptives and application techniques would likely be incentivized, and, as a result, it would become a more affordable technology and current challenges in the compromising of individual welfare would be overcome. This, in turn, would allow for more studies on the use of these contraceptives in different species, including an extensive assessment of its effects on animal welfare, both short- and long-term (Brennan 2018).

Research implications

In the last 30 years, new methods have been developed that do not entail the death of animals to prevent their populations from increasing, such as contraceptive vaccines for fertility control in wild animal populations (Jewgenow 2016). This is in line with growing interest in the protection of animals and opposition to the lethal control of them, as well as with restrictions on biocides.

The immunocontraceptive vaccination approach in wild mammal populations is simple to administer, is effective for several years, and has shown few or no side effects in treated individuals.The most recent studies demonstrate that they are safe and effective in the short term (Killian et al. 2004; 2006b). Additionally, its acceptance in society can be expected to grow, due to increasing public concern for animal welfare.

Between the two types of immunocontraception mentioned, the GnRH-type vaccines seem to be the most suitable, especially in hunted animals like deer, as they have the least impact on animal welfare (Hampton et al. 2015). These vaccines could entail at least a partial solution to the problem of managing population excesses in deer living near cities and small population centers (Gionfriddo et al. 2006).

In coming years, more studies are needed on: (1) development of effective methodologies for remote vaccine delivery, (2) development of vaccines from bacterial cultures or *plant-based* baits, and (3) the impact and efficacy of immunocontraceptives in other less-evaluated taxa.

We suggest that a greater effort is justified for developing less invasive and non-lethal population control modalities. The current theoretical framework allows progress in the development of population control taking individual animals into account. The implementation of future scientific studies will produce results of high interest for the scientific community. Thus, the development of immunocontraceptive vaccines will improve as time goes on and its progress will contribute to the welfare of individual animals.

Studies such as this review aim to facilitate the dissemination of the information collected by the scientific community to date on contraception as a tool to manage the increase in wild animal populations in a way that does not cause harm to them.

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