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Review

Bridging reproductive management and ecosystem function: behavioural pathways linking contraception to zoogeochemistry

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Abstract

Fertility control interventions have become a popular method of managing population growth in hyperabundant wildlife species. However, the literature reveals a range of unintended physiological, behavioural, and population-level consequences. We synthesized studies on wildlife fertility control interventions to identify these unintended consequences and their broader ecological implications. Through the lens of zoogeochemistry—the study of how animals influence the distribution and cycling of elements across ecosystems—we articulate how unintended secondary effects of fertility control impact biogeochemical processes via changed animal behaviour. Building on an existing framework, we identify four pathways through which fertility control interventions can affect ecosystem structure and function via changes to (1) animal physiology; (2) animal diet and elemental intake; (3) animal movement and activity patterns; and (4) animal community size and composition. Evidence indicates that wildlife fertility control can have unintended consequences, creating knock-on effects that alter individual animal behaviours such as diet, movement, activity, and animal community composition and abundance. We demonstrate how these changes can affect the distribution and stoichiometry of elements across landscapes, ultimately illustrating the link between birth-control-induced changes in behaviour to effects on ecosystem composition and functioning.

Key words: fertility control, wildlife contraception, hyperabundant populations, zoogeochemistry, biogeochemical cycles, wildlife management

Introduction

Hyperabundant wildlife often are implicated in human-animal conflict and can impact ecosystem function and biodiversity (Asa and Moresco 2019; Massei 2023). Fertility control is a useful method for reducing the abundance of hyperabundant wildlife by reducing fertility and population growth (Asa and Moresco 2019). Fertility control interventions, including surgical sterilization, hormonal implants, and immunocontraceptives, have various hormonal pathways and physiological mechanisms to prevent birth (see Table 1 and Appendix A for overview). However, fertility control can influence the physiology, behaviour, and populations of wildlife, leading to secondary effects within ecosystems. We examine potential ecosystem-wide effects of fertility control in hyperabundant wildlife populations, with particular attention to zoogeochemistry—the study of how animals influence the distribution and cycling of elements across ecosystems (Ellis-Soto et al. 2021; Abraham et al. 2023; Ferraro et al. 2023).

While many animal populations and species are facing increased risks of extirpation or extinction, others are experiencing population booms (McLaren et al. 2004) and are considered hyperabundant (Côté et al. 2004). Populations are often considered hyperabundant when they reach a size that may affect other species that managers or conservationists wish to prioritize. Culling wild animals, regardless of population numbers, has often been deemed ethically unacceptable (Lederman et al. 2021) and can have ecological consequences such as lost nutrients from missing carcasses, or unintended changes in population size of non-target species (Woodroffe et al. 2005; McManus et al. 2015; Ferraro and Hirst 2024). Translocating a portion of individuals to reduce local densities is another potential management strategy, but it is rarely feasible or effective at scale (Massei et al. 2010). As a result, conservationists and wildlife managers have turned to alternative methods, such as fertility control, to manage population abundance (Gray and Cameron 2010). Since the 1970s, fertility control has been used in approximately 100 captive and wild species as a presumed humane, oftentimes more feasible, practical and effective, method of regulating populations (Asa and Moresco 2019; but see Hampton et al. 2015).

Table 1. Fertility control methods used in non-provisioned wildlife species categorized by mechanism of action.

Class	Fertility control method	Description	Sex targeted	Treatment outcome
Endocrine suppressant	Castration	Removal of testes	Males	Sexual behaviours reduced, male is infertile
	Ovariectomy	Removal of ovaries	Females	Sexual behaviours reduced, female is infertile
	GnRH agonist	Binds to GnRH receptors	Females and Males	Suppressed gonadal function; sexual behaviours may be reduced, both sexes infertile
	GnRH immunocontraception	Induced immunity to GnRH	Females and Males	Suppressed gonadal function; sexual behaviours may be reduced, both sexes infertile
	Synthetic progestins	Prevents ovulation	Females	Estrus periods cease, ovulation suppressed
Physical non-endocrine	Vasectomy	Ligation of vas deferens	Males	Sexual behaviours continue, male is infertile
	Tubal ligation	Ligation of oviducts	Females	Estrus periods continue, female is infertile
	Intra-uterine device	Endometrium irritation	Females	Estrus periods continue, fertilization and implantation blocked
Chemical non-endocrine	pZP immunocontraception	Induced immunity to ovum proteins	Females	Estrus periods continue, ovulation may occur, fertilization prevented via immune response

Note: See Hampton et al. (2015) for expanded table including methods of fertility control successfully used in laboratory trials. GnRH, Gonadotropin releasing hormone; pZP, porcine zona pellucida.

Given the multiple mechanisms through which fertility control operates, its effects extend beyond reducing fertility and controlling population size. These interventions also lead to physiological, behavioral, and population-level changes—what we refer to as unintended consequences (Massei and Cowan 2014). Therefore, as with any management intervention, the unintended consequences from fertility control could, in turn, produce cascading effects, potentially impacting broader ecosystem dynamics.

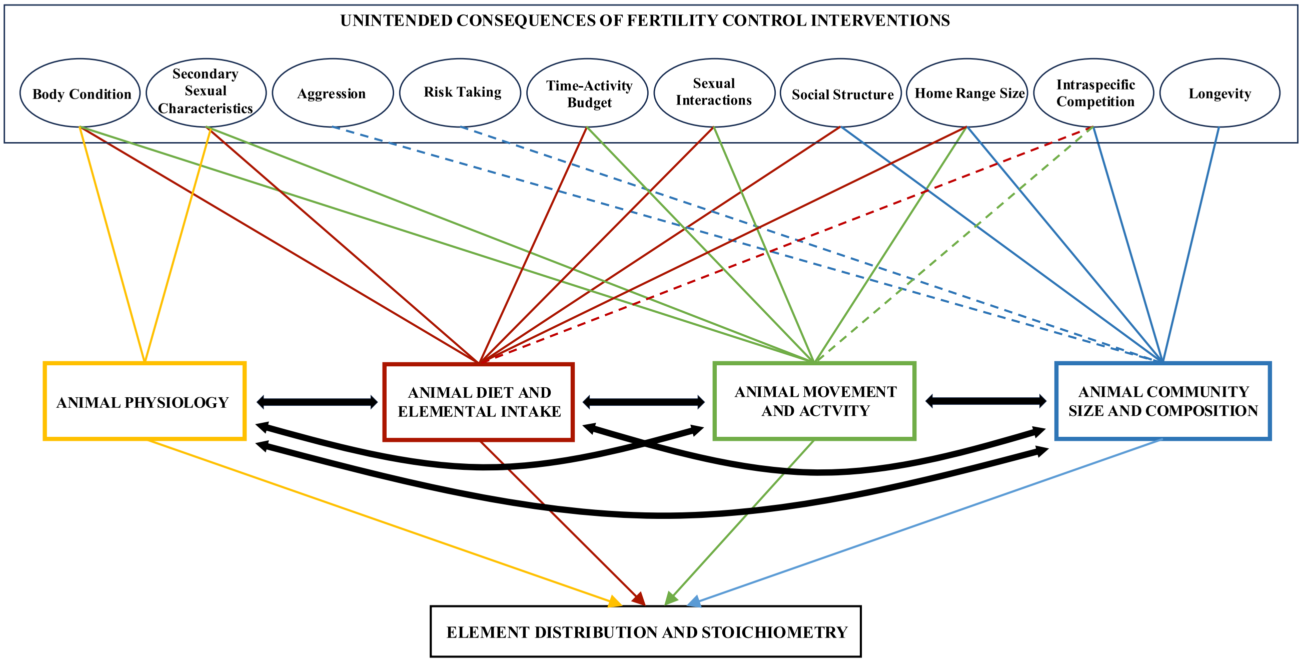
We applied the principles of zoogeochemistry to examine the unintended ecosystem consequences of fertility control, as these interventions directly affect the mechanisms that underpin animal-driven elemental processes. Our approach builds on the framework by Abraham et al. (2023) for assessing anthropogenic impacts on zoogeochemistry. Specifically, we assess how the effects of fertility control influence the extent and direction of animal-driven nutrient cycling through four key mechanisms: (1) the nutritional composition of animal bodies and waste-products, (2) animal diet and elemental intake, (3) animal movement and activity patterns, and (4) animal community size and composition (Fig. 1; Davies and Asner 2019; Sitters and Andriuzzi 2019; Ellis-Soto et al. 2021; Abraham et al. 2023; Ferraro et al. 2023; Burak et al. 2024). Fertility control could therefore influence element recycling and redistribution beyond the obvious mechanisms of population reduction, with subsequent impacts on ecosystem composition and functioning (Schmitz et al. 2018; Forbes et al. 2019; Monk et al. 2024).Of note, we do not make any judgment about the welfare standards or ethical justification of fertility control interventions in any given case, nor do we evaluate the normative value of any ecological consequence. Rather, our focus is on the mechanistic pathways through which such interventions may alter zoogeochemical processes and ecosystem dynamics without any value judgement on those consequences.

To assess possible ecosystem implications of fertility control via zoogeochemistry, we first conducted a literature review of the current fertility control methods used for managing hyperabundant wildlife populations. We present the results of this review within the context of the four key mechanisms listed above. In doing so, we highlight the potential unintended consequences of fertility control on the physiology, behaviors, and population dynamics of non-provisioned wildlife species (Fig. 2). We then explore how such side effects can influence elemental cycling and redistribution and, consequently, ecosystem functioning, again within the context of the four key mechanisms listed above. The review highlights the broader ecological consequences of wildlife fertility management and underscore the complex interconnections between population control strategies, nutrient cycles, and ecosystem health.

Review methods

We found 65 articles on fertility control interventions used in the mitigation of hyperabundant wildlife species, and 30 of these articles quantitively analyzed the unintended consequences of fertility control interventions. See supplementary materials for a full article list, and article screening and selection process. These unintended consequences encompassed a wide array of factors, including physiological changes, alterations in social behaviour, shifts in space use patterns, and population-level effects (supplementary materials Table S1). There were 11 unique species, all of which were mammals, and the majority of which (7/11; 64%) were large mammals weighing over 10 kg but less than 1 tonne as adults (supplementary materials Table S3). The most common fertility control intervention was porcine zona pellucida (pZP) immunocontraception, which was used in 42% of studies. The vast majority (27/31; 87%) of studies focused on fertility control interventions administered to females (supplementary materials Table S4).

Fig. 1. A summary of unintended consequences of fertility control interventions that effect zoogeochemical processes and nutrient cycles, modified from Abraham et al. (2023). Line type indicates if the effects are direct (solid) or indirect (dashed). The coloured lines indicate links between the unintended consequences of fertility control interventions and animal physiology (yellow) animal diet and elemental intake (red), animal movement and activity (green), and animal community size and composition (blue) working in synergy to shape the distribution and stoichiometry of elements across ecosystems.



Nutritional composition of animal bodies and waste-products

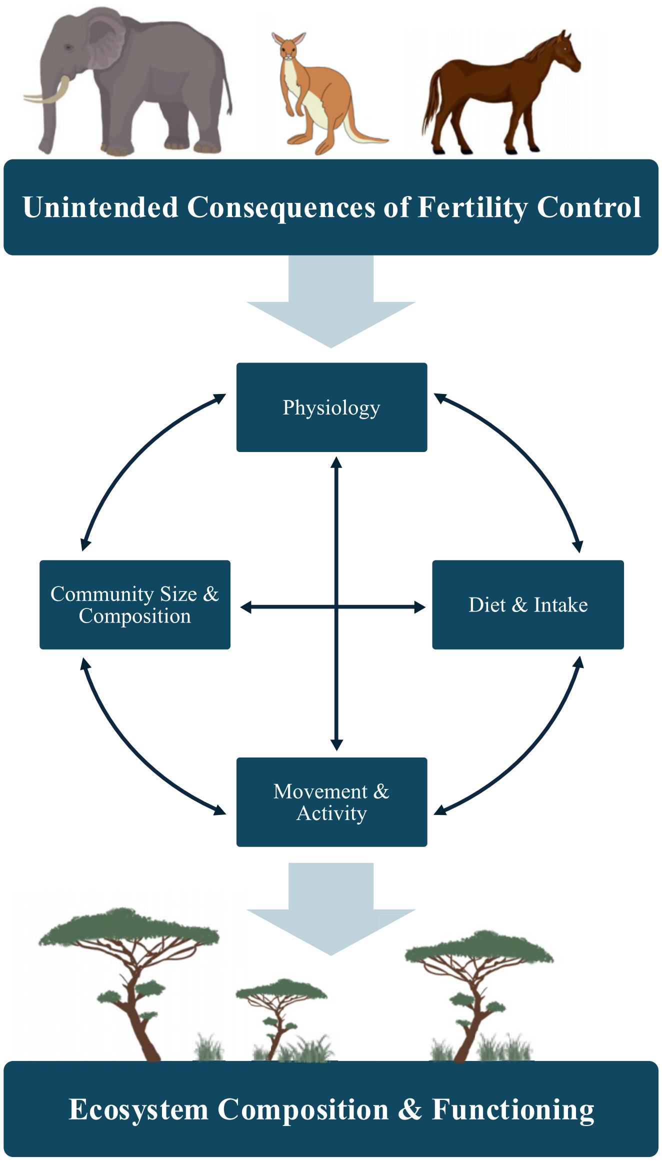
Unintended consequences of fertility control for animals

Significant modifications to an animal's overall physical condition may occur when reproductive hormone processes are disrupted by fertility control methods that suppress endocrine functioning (Table 1). For females, fertility control stops energetically demanding life history events such as gestation and lactation (Parker et al. 2009). Without investing in reproduction, individuals may increase their fat stores (McShea et al. 1997; Hampton et al. 2015). An increase in fat stores has been perceived positively or neutrally from an animal welfare standpoint, without considering the potential behavioural implications, such as changes to foraging behaviour (Hampton et al. 2015). However, there are also instances where body condition decreases substantially. In a study involving a population of free-ranging elk (*Cervus elaphus* Linnaeus, 1758), researchers observed that the use of a gonadotropin releasing hormone (GnRH) agonist resulted in treated females catabolizing proportionately more body fat during winter compared to their control counterparts, resulting in lower body condition (Conner et al. 2007). Such differences in body condition between treated and untreated individuals may be partially explained by the influence of gonadal hormones on food intake and diet (Conner et al. 2007).

Fertility control can change physical characteristics of secondary sexual traits. For instance, male white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) treated with GnRH immunocontraception developed malformed antlers that did not harden, nor shed velvet, and atrophied (Curtis et al. 2008). The loss of secondary-sexual characteristics is likely to have downstream consequences. For example, male white-tailed deer with no antlers will experience a decrease in dominance rank, impacting access to food and mates. Large antlers require sufficient nutrients to support their growth (French et al. 1956), which could also impact dietary preferences and foraging behaviour.

Changes to hormones and sex organs are also expected because fertility control interventions act directly on reproductive functioning (Fig. A1; Gray and Cameron, 2010). For instance, GnRH immunocontraception used on wild and captive male African elephants (*Loxodonta africana* (Blumenbach, 1797)) led to a decrease in testes size and accessory sex organs after multiple treatments (Lueders et al. 2017). Changes to hormones and organ structure would be important to consider within the context of reversibility if an individual is expected to return to fertility after the cessation of fertility control (Gray and Cameron 2010). Yet these types of changes are difficult to study in free-ranging, non-provisioned wildlife and, as such, are not within the scope of this review.

Fig. 2. Simplified graphical illustration demonstrating how the side effects of fertility control can impact the ecosystem through four interconnected pathways: (1) animal physiology, (2) animal diet and elemental intake, (3) animal movement and activity patterns, and (4) animal community size and composition. Changes to these mechanisms through fertility control interventions can have subsequent impacts on ecosystem composition and functioning processes.



Ecosystem level impacts of fertility control through zoogeochemical mechanisms

The physiological changes induced by fertility control could have several zoogeochemical implications. First, animal carcasses are important sources of nutrient inputs (Monk et al. 2024) that accelerate nutrient cycling (Barton and Evans 2017) and create biogeochemical hotspots across landscapes (Bump et al. 2009; Ferraro et al. 2023). Since fertility control can influence an animal's physical condition and characteristics and, consequently, the nutrient composition and stoichiometry of its body, it might indirectly affect critical nutrient contributions like carcasses. Likewise, antler sheds are significant calcium sources in many ecosystems (Gaetano et al. 2023), and the loss of this input due to fertility control could have ecosystem-level consequences.

One notable physiological impact of fertility control is the disruption of nutrient inputs from parturition by-products into ecosystems. Throughout the animal kingdom, parturition events result in the deposition of vital nutrients to ecosystems, including placenta (Roman et al. 2014), natal fluid (Ferraro et al. 2023), eggs (Helfield and Naiman 2001), and carcasses (Ferraro et al. 2024). For example, salmon swim from marine environments to freshwater streams to spawn. The nutrients from eggs and carcasses at these spawning sites lead to high amounts of nitrogen and phosphorus (Helfield and Naiman 2001), and although juveniles migrate back down-river, the majority of nutrients from eggs and carcasses is estimated to remain at the site (Moore and Schindler 2004). Thus, salmon spawning transports nutrients counter-directionally to abiotic factors (e.g., river currents). These nutrients support both the aquatic and terrestrial food webs (Moore and Schindler 2004; McInturf et al. 2019). By preventing reproductive events, fertility control directly reduces such nutrient inputs, potentially altering ecosystem dynamics and feedbacks (Auer et al. 2018; Ferraro et al. 2024).

Similarly, when large mammals exhibit site fidelity to calving locations, the nutrients deposited through natal fluids, placentas, carcasses, and in some cases antlers, can potentially improve plant quality for extended periods of time (Ferraro et al. 2023; Miller et al. 2023; Ferraro et al. 2024). Site fidelity may lead to a positive zoogeochemical cycle, where nutrients previously deposited during calving become bioavailable during lactation (Ferraro et al. 2024). If only a small proportion of the population is giving birth, lack of nutrient deposits from parturition could have further implications for plant growth and ecosystem functioning. Fertility control is often used when the effects of overpopulation become apparent, such as over-browsing, landscape transformation, or erosion, and potentially stripping the ecosystem of nutrients by decreasing births needs to be considered within the context of ecosystem restoration and conservation.

Animal diet and elemental intake

Unintended consequences of fertility control for animals

Fertility control can impact body condition and animals physiology, and such shifts may lead to changes in diet and foraging behaviour as animals adjust to meet their nutritional needs (Birnie-Gauvin et al. 2017). For example, in elk, a positive relationship between strength of selection for forage quality and nutritional condition in certain seasons has been observed (Long et al. 2014). Animals in poorer body condition may shift their foraging strategies to prioritize higher-calorie or nutrient-dense food sources, even at the expense of riskier foraging behaviour and predation (David et al. 2012; Ladds et al. 2020). Therefore, fertility control that decreases body condition (e.g., Conner et al. 2007), will likely influence diet and foraging behaviours. Conversely, using fertility control to alter reproductive hormones and reducing energetically demanding life stages like gestation and lactation, can increase fat stores in treated animals (Hampton et al. 2015). Improved body condition could reduce the urgency to seek out nutrient-rich forage.

If fertility control intervention is effective at reducing the population size, there may also be a reduction in intraspecific competition for food and territory (Watters et al. 2021). With fewer individuals competing for resources, treated populations may gain access to higher-quality forage, spend more time foraging in previously contested areas, or shift foraging strategies. Additionally, intraspecific competition is positively correlated with cortisol levels (Zhou et al. 2020), meaning a reduction in intraspecific competition could lower stress levels of the treated populations. Decreased stress levels could potentially influence body condition and metabolic rates, which can lead to changes in diet and foraging behaviour.

Ecosystem level impacts of fertility control through zoogeochemical mechanisms

Changes in diet from fertility control interventions could have cascading effects on nutrient recycling. Through foraging, animals can modify the quantity and quality of resources entering the soil, which, in turn, can affect the rate of organic matter decomposition and the availability of soil nutrients (Bardgett and Wardle 2003). For example, elk that consume plants with higher nitrogen content release a larger proportion of nitrogen through their urine (Hobbs 1996). In boreal forests, high rates of moose (*Alces alces* (Linnaeus, 1758)) browsing changed plant communities and litter quality, depressing nitrogen mineralization and net primary production (Pastor et al. 1993). If fertility control leads to shifts in foraging strategies, ecosystems may experience changes in plant community composition and subsequent litter inputs—leading to changes in elemental cycling and availability. Additionally, changes in foraging strategies can alter elemental content released through urine and excrement (Bardgett and Wardle, 2003). Therefore, in addition to the direct impacts that changes in an animal's body condition could have on zoogeochemistry, changes in foraging strategies could also initiate indirect impacts.

While the impact of stress on animal zoogeochemical inputs has primarily been demonstrated in the context of predation (Hawlena and Schmitz 2010) or nutritional stress (Saltz and White 1991), changes to hormones from fertility control may have similar implications. Stress can change metabolic demands for animals, leading to increased carbohydrate consumption and changes in the C:N ratios in bodies, urine, and fecal matter (Saltz and White 1991; Christensen and Creel 2010; Hawlena and Schmitz 2010). For example, the excreta and decomposition of stressed grasshoppers (*Melanoplus femurrubrum* (De Geer, 1773)) differs in stoichiometry from non-stressed individuals, which has demonstrated implications for soil microbial communities and composition (Schmitz 2003; Yang and Gratton 2014). Similarly, in the presence of wolves, the urine nitrogen content for elk decreased, likely due to changes in forage patterns (Christianson and Creel 2010).

Animal movement and activity patterns

Unintended consequences of fertility control for animals

Numerous examples in the literature demonstrate that fertility control can impact both social and spatial behaviours in wildlife populations (Table 2). In wild African elephants, for example, the use of GnRH immunocontraception prevents males from entering periods of heightened sexual activity—known as musth. Musth is characterized by an increase in testosterone and energy levels, resulting in heightened aggression and risk-taking behaviours to search and compete for potential mates (O'Connell-Rodwell et al. 2022). If aggressive and risk-taking behaviours are reduced through the suppression of musth, we would expect direct repercussions on dominance rank, since these behaviours are important in the establishment of male African elephant dominance hierarchies (Hollister-Smith et al. 2007; Doughty et al. 2014). A decrease in both competition and physical combat between males may also alter sex-ratios within a population, as male–male intraspecific combat can result in injury or mortality of the participants (Vander Linden and Dumont 2019). This may influence the number of animal carcasses as nutrient inputs across the landscape.

Changes in sexual interactions are evident, particularly when fertility control methods do not suppress endocrine functioning, allowing females to exhibit normal estrus cycles. In both wild horse and elk populations, females treated with pZP immunocontraception receive significantly more courtship behaviours and sexual interactions from males than their untreated counterparts, likely due to continued or extended estrus cycling (Heilmann et al. 1998; Ransom et al. 2010). Increases in sexual interactions, courtships, and mating behaviours would likely change time-activity budgets of both males and females, which may have further implications for movement if the sexual interactions are taking place outside of the breeding season, where (in most ungulate species) the sexes segregate and live in different groups outside of the breeding season (Ruckstuhl and Neuhaus 2000). Continued estrus cycling or extended estrus periods in females may lead to an increase in physical activity of males from courtship, intraspecific competition, and mating behaviours (Woodward et al. 2006), all of which would spatially influence nutrient deposition.

Fertility control interventions can also alter home range size. Female koalas (*Phascolarctos cinereus* (Goldfuss, 1817)) treated with synthetic progestin implants increase their long-range movements (Hynes et al. 2011). In another study, wild female ricefield rats (*Rattus argentiventer* (Robinson & Kloss, 1916)) were either surgically sterilized via tubal ligation, given synthetic progestin implants, or left as controls. The surgically sterilized rats had the largest home ranges, nearly

Table 2. Summary of unintended consequences by fertility control intervention and species.

Unintended consequences	Fertility control intervention	Species (Scientific name)	Reference
Aggression and risk taking	GnRH immunocontraception	African elephant (*Loxodonta africana*)	(Lueders et al. 2017)*, (Nys et al. 2010)*
Body condition	GnRH agonist	brushtail possum (*Trichosurus vulpecula* (Kerr, 1792))	(Lohr et al. 2009)
		elk (*Cervus elaphus*)	(Conner et al. 2007)
		lion (*Panthera leo* (Linnaeus, 1758))	(McEvoy et al. 2019)
	Synthetic progestin	eastern grey kangaroo (*Macropus giganteus* Shaw, 1790)	(Nave et al. 2002)
	Tubal ligation	koala (*Phascolarctos cinereus*)	(Watters et al. 2021)
	pZP immunocontraception	fallow deer (*Dama dama* (Linnaeus, 1758))	(Fraker et al. 2002)
		wild horse (*Equus caballus*)	(Kirkpatrick and Turner 2008)
	GnRH immunocontraception	elk (*Cervus elaphus*)	(Conner et al. 2007)
Home range	pZP immunocontraception	white-tailed deer (*Odocoileus virginianus*)	(Hernandez et al. 2006)
	Synthetic progestin	koala (*Phascolarctos cinereus*)	(Hynes et al. 2011)
		ricefield rat (*Rattus argentiventer*)	(Jacob et al. 2004)
	Tubal ligation	ricefield rat (*Rattus argentiventer*)	(Jacob et al. 2004)
Intraspecific competition	Tubal ligation	koala (*Phascolarctos cinereus*)	(Watters et al. 2021)
Secondary sexual characteristics	GnRH immunocontraception	white-tailed deer (*Odocoileus virginianus*)	(Curtis et al. 2008)*
Sexual interactions	pZP immunocontraception	white-tailed deer (*Odocoileus virginianus*)	(Miller et al. 2001)
		elk (*Cervus elaphus*)	(Heilmann et al. 1998)
		wild horse (*Equus caballus*)	(Ransom et al. 2010), (Nunez et al. 2009)
	GnRH agonist	eastern grey kangaroo (*Macropus giganteus*)	(Woodward et al. 2006)
		lion (*Panthera leo*)	(McEvoy et al. 2019)
	GnRH immunocontraception	wild horse (*Equus caballus*)	(Baker et al. 2018)
Social structure	GnRH agonist	lion (*Panthera leo*)	(McEvoy et al. 2019)
	GnRH immunocontraception	African elephant (*Loxodonta africana*)	(Doughty et al. 2014)*
		wild horse (*Equus caballus*)	(Baker et al. 2018)
	pZP immunocontraception	wild horse (*Equus caballus*)	(Madosky et al. 2010), (Turner and Kirkpatrick 2002), (Nunez et al. 2009)
Time-activity budget	GnRH immunocontraception	wild horse (*Equus caballus*)	(Ransom et al. 2014*a*)
	Synthetic progestin	eastern grey kangaroos (*Macropus giganteus*)	(Poiani et al. 2002)
Longevity	pZP immunocontraception	wild horse (*Equus caballus*)	(Kirkpatrick and Turner 2008)

Note: All fertility control interventions were administered to females, with the exception of where references are marked with an asterisk (*). Some articles explore multiple types of fertility control, or document more than one unintended consequence, as such, some references are listed more than once. GnRH: Gonadotropin releasing hormone; pZP: porcine zona pellucida.

twice the size of the hormonally contracepted and control group ranges. Female rats with synthetic progestin implants exhibited a high rate of burrow relocation, indicating potential territory loss (Jacob et al. 2004). The size of an animals' home range and its movement within this area, directly influence its access to food resources, interactions with predators, and mating opportunities (Herfindal et al. 2009; Ofstad et al. 2016). Significant increases or decreases in home range size could, therefore, lead to individual differences in fitness between treated and untreated individuals (Ofstad et al. 2016), generating spatio-temporal variation in population composition (Lande et al. 2003; Banks and Lindenmayer 2014). Consequently, alterations in home range size or movement patterns following fertility control could influence the likelihood of wildlife entering anthropogenic areas, elevating the risk of motor vehicle collisions and other human-wildlife conflicts.

Finally, evidence suggests that time-activity budgets can be affected by fertility control. Differences in females' behaviours are consistent with the metabolic needs of non-gestating versus gestating/lactating females (Ransom et al. 2010). For example, wild female horses treated with a GnRH immunocontraception reduced the time spent eating and traveling, while increasing the time resting and engagement in maintenance behaviours compared to untreated females (Ransom et al. 2014*a*). Changes to time-activity budgets, specifically changes to foraging and movement, would likely have downstream effects that influence ecosystems through zoogeochemical mechanisms.

Ecosystem level impacts of fertility control through zoogeochemical mechanisms

Social and spatial behaviours in wildlife populations can have shared consequences for ecological processes (Webber et al. 2022). The unintended social and spatial behavioural changes resulting from fertility control interventions could cascade through wildlife populations, affecting dominance structures, sex ratios, activity budgets, and home range dynamics. Animals translocate nutrients directly across landscapes via their excreta and carcasses, and also indirectly, through ecosystem engineering, seed dispersal, and trampling (Subalusky et al. 2017; Schmitz et al. 2018; McInturf et al. 2019; Abraham et al. 2023). The unintended consequences of fertility control interventions—such as changes in social behaviours, altered spatial movements, and changing time-activity budgets—likely have cascading effects that influence ecosystems through zoogeochemical processes. By altering where and how animals move, forage, and deposit nutrients, these changes can alter nutrient flows, impacting habitat composition and ecosystem functioning (Ellis-Soto et al. 2021).

Terrestrial vertebrates, which are currently the only group of animals represented in our literature review on fertility control, are considered disproportionately important for lateral element transport (Subalusky et al. 2017), and have been labelled “nutrient arteries” for the planet (Wolf et al. 2013). One extreme example is species that migrate spatially and temporally. Through migration, animals influence the distribution of nutrients as they transport nutrients between distinct locations (McInturff et al. 2019). For instance, the annual mass migration of ∼1.2 million wildebeest (*Connochaetes taurinus* (Burchell, 1823)) through the Serengeti Mara ecosystem includes crossing the Mara River, where mass drownings occur resulting in large influxes of nutrients into the local river systems (Subalusky et al. 2017). Upon reaching their location, migrants contribute nutrients in the form of excrement (urine/feces), reproductive material, or carcasses, which can lead to a net flux of nutrients at an arrival site (Holdo et al. 2011; Ferraro et al. 2024). Given that some animals do not migrate when population sizes are smaller (Lundberg 1988; Taylor and Norris 2007), fertility control may cause this nutrient artery to be lost.

Even at smaller scales, the redistribution of nutrients from animals as they forage, defecate, and ultimately die can influence nutrient cycles, shape nutrient stocks, and ultimately create patterns of landscape heterogeneity (Bump et al. 2009; Ferraro et al. 2023; Monk et al. 2024). It is, therefore, likely that changes in home ranges from fertility control would change the distribution of nutrients at large and small scales.

Many social animals aggregate in spatially explicit ways. Whether aggregating behaviour occurs on a daily (e.g., foraging behaviour) or seasonal (e.g., breeding) basis, can also affect the nature and magnitude of nutrient distribution across landscapes (McInturf et al. 2019; Ferraro et al. 2023). For example, social information may lead to the correlation of spatial and social behaviours of multiple individuals (Gil et al. 2018). Breeding site-selection by gregarious species is often based on cues about local breeding condition from conspecifics (McInturf et al. 2019). If the same breeding-site is used, fluctuations in population density, or changes in group composition (e.g., ratio of reproductively active individuals) due to the use of fertility control, will lead to changes in nutrients deposited at a site. Temporal synchrony of specific behaviours can also influence nutrient deposition. For example, calving in ungulates is synchronous, leading to an episodic pulse of high-quality resources from parturition (Ferraro et al. 2024), which again, would be influenced by the community size and composition changing after fertility control intervention. Similarly, social behavior of latrine use can create hotspots of nutrient pulses (Monk et al. 2024).

Animal community size and composition

Unintended consequences of fertility control for animals

Population-level effects are documented throughout the fertility control literature. In particular, a direct and intended implication of fertility control is a reduction in population density. However, changes in population density, regardless of how they are achieved (e.g., culling, translocation, fertility control) may lead to indirect demographic and ecological effects that must be considered when managing a population. For instance, female koalas sterilized via tubal ligation experienced a decrease in intraspecific competition for food and territory (Watters et al. 2021). A decrease in intraspecific competition or increased body condition may also positively influence population-wide longevity. For example, when female horses were treated with pZP immunocontraception, both female and foal mortality rates dropped significantly below historic and pre-treatment levels, resulting in a new age structure with different relative proportions in each age class within the treated populations (Turner and Kirkpatrick 2002). Altered age classes and population structures would presumably result in individuals of differing nutrient composition and stoichiometry, and metabolic rates compared to untreated counterparts, leading to changes in diet and foraging behaviour, and nutrient output into the ecosystem.

Group formation and social structure are also influenced in various species. In the case of wild horses, a harem consists of a dominant adult male, several females, and their immature offspring (McDonnell and Murray 1995). In one study, females treated with pZP immunocontraception visited and changed harem groups more frequently than untreated females (Nunez et al. 2009). In a subsequent study, contracepted females were compared to females that were previously treated (but no longer on contraceptives), and both groups continued to change harems at a higher frequency than controls, indicating behavioural side-effects may not be easily reversed (Madosky et al. 2010). Female lions given GnRH agonists have also been reported to display behavioural changes resulting in group fragmentation (McEvoy et al. 2019). GnRH immunocontraception can also influence

Box 1. Exploring policy discourse in population control programs—wild horses in North America as an example.

Wild horses are considered by some experts as native species in North America, embedded with wildness, ancient behavioral patterns, and the morphology and biology of a sensitive prey species (Kirkpatrick and Fazio 2010). However, others consider them "non-native," "feral," or even "exotic" species, descended from the earliest-known instance of horse domestication by humans. Such labels such as "native" and "non-native" have important management implications, especially in management programs that prioritize the protection and conservation of native species. As population densities increase, wild horses are becoming important and dominant drivers of change within their environment (Boyce and McLoughlin 2021). Although the debate of "native" versus "non-native" is ongoing, hyperabundance of wild horses and threats to biodiversity has led to the adoption of laws in the United States considering wild horses as "pests" (Nimmo et al. 2007). This status allows for the implementation of lethal intervention programs such as culling (Górecka-Bruzda et al. 2020).

Many experts argue that within the context of conservation the "native" label can be uninformative and counterproductive (Coghlan and Cardilini, 2022). Non-native species may benefit local communities, by safeguarding against species extinction, or restoring ecosystem functioning (Lundgren et al. 2018; Wallach AD et al. 2020). Rather than focussing on labelling a species as "native" or "non-native," or "pests," conservationists and wildlife managers should determine whether species are benefiting or harming biodiversity, ecological functions, and/or human health (Davis et al. 2011). However, the debate continues, with the need for a sustainable management plan being a common point of agreement among stakeholders. The challenge lies in balancing the cultural significance of wild horses, their ecological impact, and the practicalities of population control.

herd social structure when administered to male African elephants. Treated adult males spent abnormally high amounts of time with the family unit, rather than forming bachelor herds or roaming independently compared to untreated male counterparts (Doughty et al. 2014). Atypical group size or social structure, i.e., fragmentation would impact redistribution of nutrients from individual animals, shaping nutrient stocks and ecosystem composition.

Ecosystem level impacts of fertility control through zoogeochemical mechanisms

Changes to wildlife composition and abundance can reshape ecosystem stoichiometry and elemental distribution (Ferraro and Hirst 2024). If a certain species within a community is reduced (e.g., local extinctions) or promoted (e.g., conserved species), or introduced (e.g., non-native species), the nutrient deposition patterns will be influenced. A notable example is the drastic decline in wild vertebrate biomass, which has reduced the global transport of nutrients by these animals to less than 10% of what it was during the late Pleistocene (Doughty et al. 2016; Abraham et al. 2023).

Megaherbivores are especially important in the local redistribution of nutrients, too. For instance, many megaherbivores play a critical role in redistributing nutrients by feeding in open habitat and defecating more evenly across the risk-gradient (le Roux et al. 2018). If elephants or other megaherbivores are treated with fertility control and the populations within a community decline, we can expect a greater accumulation of nutrients in open and less-risky habitats, with cascading consequences on vegetation and ecosystem.

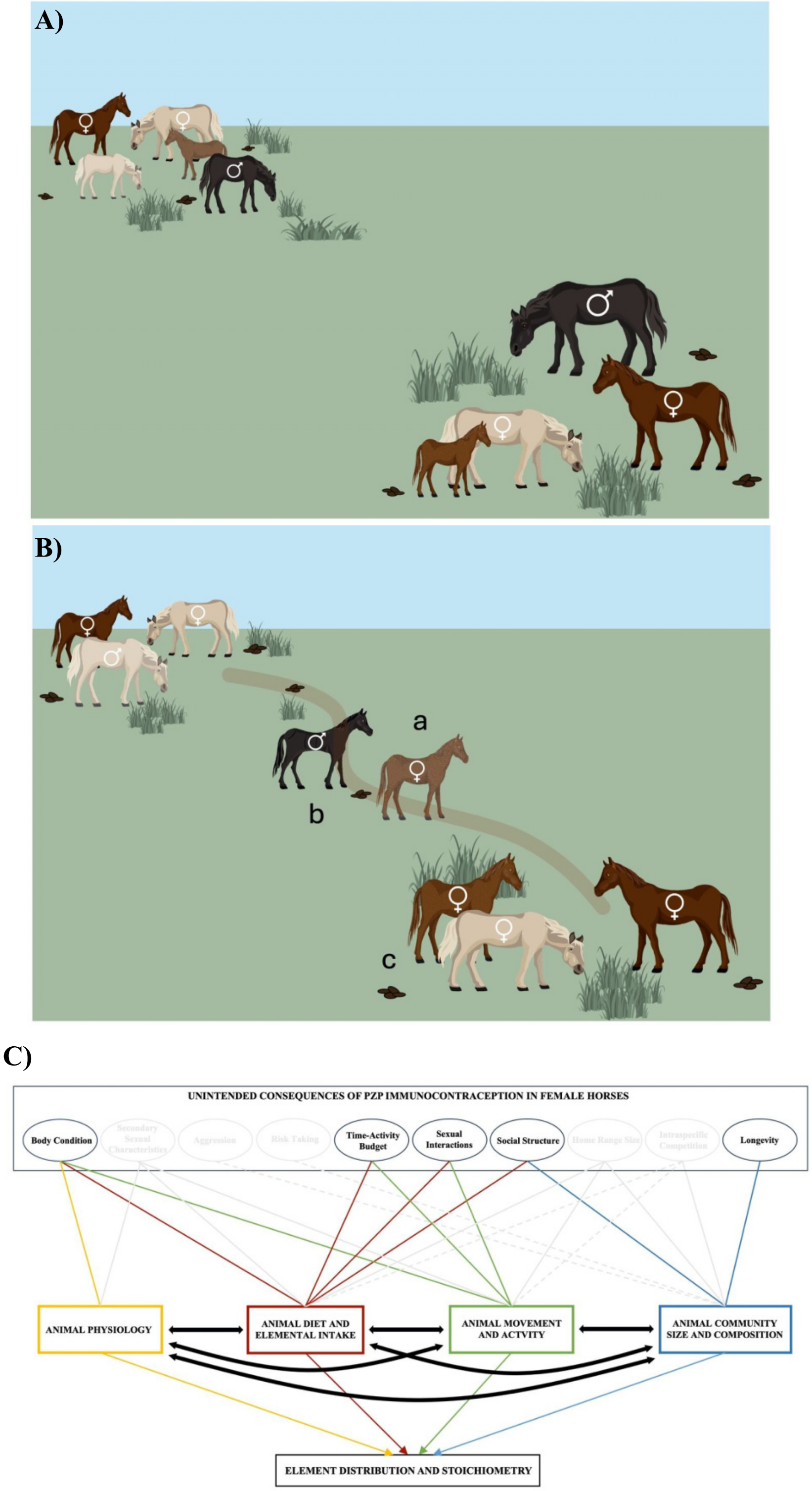
Case studies

We provide two case studies to demonstrate how unintended consequences of fertility control interventions in wild horses and African elephants can influence animal physiology, diet, movement, and community composition and the downstream implications for the ecosystem. Wild horses (*Equus caballus* Linnaeus, 1758) and elephants were chosen as they had the highest number of articles ($n = 7$ each, supplementary materials Figure S2) of any species within the examined articles.

Wild horses (*Equus caballus*)

Wild horses in North America (Box 1) live in harems consisting of a dominant adult male, several females, and their immature offspring (McDonnell and Murray 1995). The seasonal breeding behaviour of wild horses involves specific social dynamics and competition during the mating season (Górecka-Bruzda et al. 2023). Fertility control interventions, primarily the administration of pZP immunocontraception to females (Fig. 3), have been implemented to manage wild horse populations. However, several side effects have been observed, including increased sexual interactions among treated females and males, elevated rates of harem switching, and extended longevity, resulting in the emergence of new age classes (Turner and Kirkpatrick 2002; Nunez et al. 2009; Madosky et al. 2010). These unintended consequences have the potential to influence nutrient redistribution within ecosystems. Increased sexual interactions and more frequent harem switching, for example, will alter the spatial distribution of nutrient-dense excreta due to changes in mating behaviour and movement patterns. There is high pressure from external males during the breeding season, and the dominant male will spend more time in vigilance and locomotion and less time foraging compared to females (Duncan 1980; Górecka-Bruzda et al. 2023). If treated females continue estrus cycling or exhibit extended estrus periods outside of the breeding season, this could impact male body condition, as males may continue expending energy on movement, vigilance, and competition. In herbivores, body condition can influence habitat and forage quality selection (Birnie-Gauvin et al. 2017), and males in harems with treated females may forage differently than males without treated females present.

Fig. 3. (A) An untreated population of wild horses, with two distinct harems. Adults are labelled by sex; non-adults are unlabeled. (B) A population of wild horses where females are treated with pZP immunocontraception. Compared to the untreated population, unintended consequences of fertility control may include (a) increased rates of harem switching, changing the spatial distribution of nutrient dense excreta, (b) increased sexual activity, leading to higher vigilance and mate guarding behaviour in males, which could decrease male body condition (c) an emergence of a new age class, influencing the total nutrient input as well as the ratios of nutrients supplied to the soil and plant communities. (C) Unintended consequences of pZP immunocontraception in female horses. Coloured lines indicate links between the unintended consequences of fertility control interventions and animal physiology (yellow) animal diet and elemental intake (red), animal movement and activity (green), and animal community size and composition (blue) working in synergy to shape the distribution and stoichiometry of elements across ecosystems. pZP: porcine zona pellucida.



Extended longevity and different compositions of age class categories may also influence foraging patterns and diet. For instance, an aging population will have different diet requirements compared to groups with larger proportions of young. Herbivores use nutrients in set stoichiometric ratios, that vary with body size, and such differences in the ratios at which nutrients are used leads to differences in the ratios at which nutrients are deposited through urine and feces (le Roux et al. 2020). Thus, if the average body size of the community changes, it will also influence the total input as well as the ratios of nutrients supplied to the soil and plant communities.

Changes to wild horse movement, diet, composition, or abundance, may also influence the behaviours of other large ungulates or predators, with downstream implications on zoogeochemistry. Wild horses generally co-exist with other large ungulates but tend to dominate resources and influence both spatial and temporal use of resources by other species (Hall et al. 2018). A decrease in wild horse abundance, or a change in space use, would likely shift resource use of other large ungulate species within the community. Wild horses have been recorded as being preyed on by cougars (*Puma concolor* (Linnaeus, 1771)) and wolves (*Canis lupus* Linnaeus, 1758)), but predators alone are unable to effectively reduce the population of wild horses in North America (Andreasen et al. 2021; Górecka-Bruzda et al. 2023). Young foals under one year old are most at risk of predation, however, an aging population with less young may alter direct consumptive effects of predation. Females changing harems frequently are also more at risk of predation as they move between groups, potentially influencing the spatial distribution of nutrients through excreta and carcasses (Bump et al. 2009).

African elephants (*Loxodonta africana*)

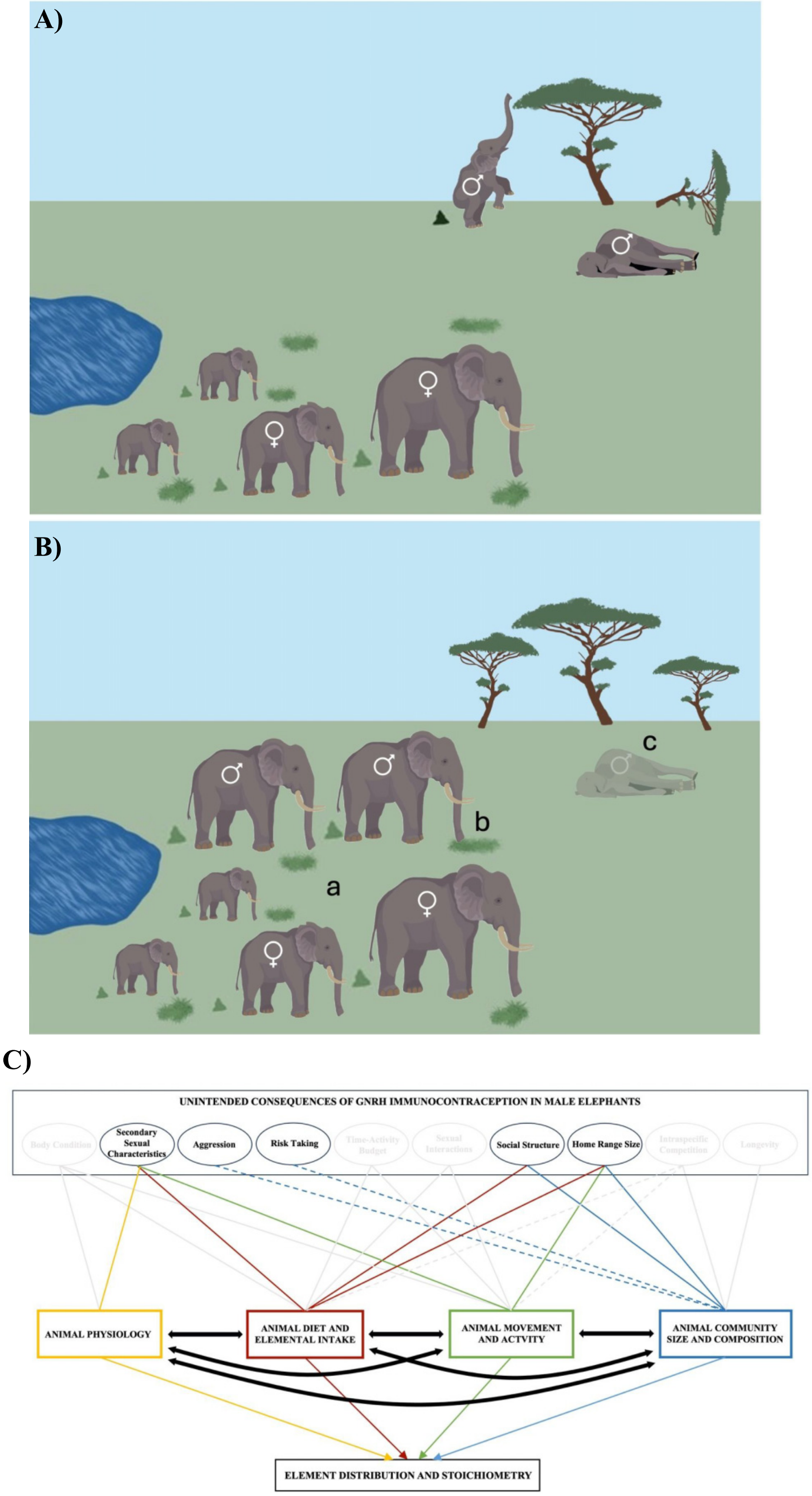
African elephants (hereafter elephants) are keystone species, having disproportionate effects on their ecosystem relative to their abundance (Shoshani et al. 2004) and are proposed to be among the main drivers of transforming woodland into savannah grasslands (Owen-Smith et al. 2019). Elephants are both browsers and grazers (Kos et al. 2012), spend the majority of their day actively foraging (Shannon et al. 2008), and consume fibrous bark, roots, leaves, and grasses. Elephants tend to be bulk-feeders; however, pronounced sexual dimorphism in body size between males and females leads to divergent foraging strategies, where females are more selective feeders (Shannon et al. 2006). Elephants have the capacity to directly influence plant mortality through toppling, debarking, trampling, or uprooting plants (Owen-Smith et al. 2019), which can, in turn, influence vegetation structure such as tree height and plant species composition (Smallie and O'connor 2000). Plant species vary in nutrient content, and changes to plant species composition within an ecosystem would presumably alter nutrient content within the standing biomass (Schmitz et al. 2018). Elephants also redistribute nutrients across landscapes, by consuming large quantities of forage (approximately 300 kg per day for adult males; Laws 1970), and excreting seeds and nutrients into the soil. Adult male elephants (but not family units) have been shown to be a dominant driver of change in aboveground carbon stocks (Davies et al. 2018).

The use of GnRH immunocontraception on male elephants (Fig. 4) has been documented to lead to changes in social structure, where males spend atypical amounts of time with the family unit (Doughty et al. 2014), decreases in aggressive behaviour, and a failure to enter periods of musth (Nys et al. 2010; Lueders et al. 2017). These unintended consequences are relevant within the context of the zoogeochemical framework and nutrient redistribution. Movement and activity patterns vary between adult males and the family units, where family units move lesser distances and use habitat differently (e.g., young elephants need to drink water more frequently, and family units spend more time near watering holes compared to adult males; Poole 1996). When treated adult males modify habitat use by spending more time with the family unit compared to their untreated counterparts (Doughty et al. 2014), it can have downstream implications on diet and movement. For instance, adult males residing within family units may employ female-typical foraging strategies (i.e., being more selective and selecting shorter vegetation). Regarding the redistribution of nutrients, this suggests that treated adult males are moving to areas frequented by females, engaging in foraging behaviour, excreting nutrients, and spatially dispersing seeds differently than if they were untreated.

If treated males are choosing plants of lesser heights, and not pushing over as many trees as untreated adult males, this may also influence the community composition of plants, having further implications on ecosystem functioning and potentially carbon storage (Davies et al. 2018). Changes to space use, such as decreased movement would also lead to reduced trampling of plants and soil. Like many terrestrial vertebrates, elephants have the ability to compact and disturb surface sediments, which can modify surface temperatures and chemical reactions, either fostering soil or sediment carbon retention or exacerbating carbon release (Schmitz et al. 2018). If treated males are consistently spending time with family units, home ranges would be smaller, and distance travelled would be less than if they were travelling alone (Smit et al. 2007), spatially modifying such soil perturbations. Treated males have been observed to be less aggressive and fail to enter periods of musth, where males experience heightened testosterone levels and increase their movement and risk-taking behaviours to compete and find mates. A decrease in risk-taking behaviour, movement, and sexual competition may lead to decreased mortality rates among treated adult males, which would result in fewer carcasses across the landscape.

A lack of young animals in the group, which could result from a variety of fertility control interventions, could also influence nutrient redistribution. The family unit prefers areas close to water with adequate tree cover (Smit et al. 2007), owing to shade and higher-quality forage requirements for young (Laws and Parker 1968; du Toit 1995). If there are no longer young individuals within the group, less time may be spent in close proximity to watering holes and high-quality forage areas, decreasing the transport of nutrients and seeds to these locations. Such changes to movements may alter plant biomass (if there is less time spent foraging and fewer

Fig. 4. (A) An untreated population of African elephants, where the family unit is separate from an all-male group. Adults are labelled by sex; non-adults are unlabeled. (B) A population of elephants where males are treated with GnRH immunocontraception. Compared to the untreated population, unintended consequences of fertility control may include (a) adult males spending atypical amounts of time with the family unit and failing to segregate, (b) using habitat differently and employing female-typical foraging strategies, and (c) decreases in aggression and risk-taking behaviour leading to decreases in male mortality rates. (C) Unintended consequences of GnRH immunocontraception in male elephants. Coloured lines indicate links between the unintended consequences of fertility control interventions and animal physiology (yellow) animal diet and elemental intake (red), animal movement and activity (green), and animal community size and composition (blue) working in synergy to shape the distribution and stoichiometry of elements across ecosystems. GnRH, Gonadotropin releasing hormone.



seeds dispersed) and animal subsidies (excrement) in these previously preferred areas.

Discussion

Fertility control interventions are increasingly employed for managing hyperabundant wildlife populations. However, these interventions may produce unintended physiological, behavioral, and population-level consequences that extend beyond individual animals to influence broader ecological processes. Our analysis identified potential consequences of fertility control in non-provisioned wildlife species, including changes to body condition, secondary sexual characteristics, aggression, risk-taking, time-activity budgets, sexual interactions, social structure, home range size, intraspecific competition, and longevity. Such changes can directly or indirectly influence animal body composition, diet, movement, activity, and population composition and abundance, as illustrated in Fig. 2. Given that animals influence their environments via many direct and indirect processes (Schmitz et al. 2018; Forbes et al. 2019; Monk et al. 2024), we further explored how fertility control could have knock-on effects on ecosystems, using zoogeochemistry as an example. Specifically, we illustrate how changes in animal characteristics influence the distribution and stoichiometry of elements across landscapes (Abraham et al. 2023). As such, these unintended effects of fertility control interventions can alter element distribution and, consequently, ecosystem composition and functioning.

There are two major gaps within the fertility control literature that became apparent through this review. First, although we found 65 studies (listed in supplementary materials) interested in demonstrating the efficacy of fertility control interventions used in wildlife populations, only 35 studies were concerned with quantitatively addressing unintended consequences within the context of hyperabundance. Many studies were also of limited sample size due to logistical challenges of fertility control administration and monitoring. Some studies that did address unintended consequences and claimed no side effects, were qualitative or anecdotal (e.g., Turner et al. 1996; Rosenfield et al. 2019), a trend also common for fertility control studies in captive populations (Gray and Cameron 2010). Second, all studies we examined focused on mammals, reflecting their prominence in wildlife management and the availability of established fertility control methods. However, as fertility control interventions gain popularity, they are increasingly being explored for other taxa, including fish and insects (Patil et al. 2014; Vargas-Terán et al. 2021). Expanding fertility control to non-mammalian species introduces new considerations, as these taxa differ significantly in reproductive strategies and ecological roles, underscoring the need for further research to assess broader ecological implications.

Generally, the goal of contraception use in non-provisioned wildlife species is to modify population dynamics, making it imperative to understand and predict population-level effects. For example, increased body condition may drive increased longevity, which can reduce the functional role of fertility control in reducing population size, and the relationships between unintended consequences need to be further disentangled. To do this, we must also determine whether unintended consequences are a result of the fertility control method itself, or a result of absence of offspring and energetically demanding life stages such as gestation and lactation. Compensatory density-dependent mechanisms also warrant attention. If population density decreases, it may lead to increased survival, improved breeding success of untreated females, or increased immigration to the area of lower density and thus higher relative resource availability (Watters et al. 2021). Increased survival and breeding success may result in a need to treat higher proportions of the population to slow population growth, which may be logistically challenging in wildlife settings (Ransom et al. 2014*b*).

Much fertility control research has focused on small populations and limited areas (e.g., Conner et al. 2007; Nunez et al. 2009; Doughty et al. 2014), but implementing fertility control on larger scales requires serious consideration. For instance, side effects and reversibility of the pZP vaccine can change depending on the number of treatments an individual receives. Wild female horses that received 4–6 treatments of pZP are more likely to display atypical band behaviour compared to females that have received 1–3 or 0 treatments (Nuñez 2018). Females that have received fewer treatments are also more likely to return to fertility after the cessation of fertility control treatment (Nuñez et al. 2017). With large-scale administration, it may not be possible to track individual treatment history or estimate population fertility or density trajectories, making it challenging to adapt to management goals. Furthermore, the effects of fertility control may only become apparent over a long time scale, especially for long-lived species where population decline and age class shifts may take years. The effects of other population management interventions, i.e., culling or translocation would be more immediate.

Given the expanding use of fertility control within wildlife management (Shuster et al. 2023; Velling et al. 2025), we demonstrate that not only do researchers need to study the welfare and efficacy of these interventions, but also any ecological consequences. In particular, we demonstrate that changes to animal physiology and behavior can influence the mechanisms through which animals affect nutrient cycling. Such shifts may alter the timing, location, or magnitude of nutrient inputs, with cascading effects on ecosystem processes and community dynamics. Zoogeochemical consequences, however, are not exclusive to fertility control; any form of population management is likely to affect how animals interact with nutrient cycles. For instance, culling has been shown to impact biogeochemical stocks (Ferraro and Hirst 2024), while hunting can alter animal movement with zoogeochemical implications (Trepel et al. 2024). Further, it is possible that fertility control has other ecosystem consequences not considered here. For example, changes in population structure, social dynamics, or interspecific interactions could reshape food webs or alter species distributions. Therefore, a thorough evaluation of any potential ecosystem outcomes is necessary to ensure that management strategies support, rather than compromise, individuals, populations, and ecosystems.

Conclusion

Fertility control can be an effective way to manage hyperabundant wildlife populations (Asa and Moresco 2019). However, this method of intervention must be critically evaluated, as fertility control can have physiological, behavioural, and population-level unintended consequences. We demonstrate how the physiological, behavioral, and population-level modifications observed in response to fertility control could have far-reaching effects beyond just changes in individual and population function, including nutrient cycling, resource distribution, and ecosystem function.

In many contexts, the benefits of fertility control intervention will outweigh the ecological consequences of uncontrolled hyperabundant populations. However, when intervention is deemed necessary, the unintended ecosystem impacts must be assessed and tabulated when developing effective and sustainable wildlife management strategies.

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The authors declare there are no competing interests.

Supplementary material

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Appendix A

Fig. A1. (A) Simplified overview of reproductive hormones, their sources, and targets, (B) Side by side overview comparing mechanisms of action and targets between the two most commonly used fertility control methods as examples. Crossed-out red circles indicate what the immunocontraception targets. Black arrows indicate normal functioning, where red arrow indicate suppressed functioning. GnRH, Gonadotropin releasing hormone; LH, Luteinizing hormone; FSH, Follicle-stimulating hormone.