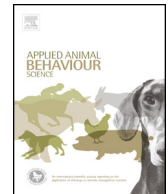




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Behavior of feral horses in response to culling and GnRH immunocontraception

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ABSTRACT

Wildlife management actions can alter fundamental behaviors of individuals and groups, which may directly impact their life history parameters in unforeseen ways. This is especially true for highly social animals because changes in one individual's behavior can cascade throughout its social network. When resources to support populations of social animals are limited and populations become locally overabundant, managers are faced with the daunting challenge of decreasing population size without disrupting core behavioral processes. Increasingly, managers are turning to fertility control technologies to supplement culling in efforts to suppress population growth, but little is quantitatively known about how either of these management tools affects behavior. Gonadotropin releasing hormone (GnRH) is a small neuropeptide that performs an obligatory role in mammalian reproduction and has been formulated into the immunocontraceptive GonaCon-BTM. We investigated the influences of this vaccine on behavior of feral horses (*Equus caballus*) at Theodore Roosevelt National Park, North Dakota, USA, for a year preceding and a year following nonlethal culling and GnRH-vaccine treatment. We observed horses during the breeding season and found only minimal differences in time budget behaviors of free-ranging female feral horses treated with GnRH and those treated with saline. The differences observed were consistent with the metabolic demands of pregnancy and lactation. We observed similar social behaviors between treatment groups, reflecting limited reproductive behavior among control females due to high rates of pregnancy and suppressed reproductive behavior among treated females due to GnRH-inhibited ovarian activity. In the treatment year, band stallion age was the only supported factor influencing herding behavior ($P < 0.001$), harem-tending behavior ($P < 0.001$), and agonistic behavior ($P = 0.02$). There was no difference between the mean body condition of control females (4.9 (95% CI = 4.7–5.1)) and treated females (4.8 (95% CI = 4.7–4.9)). Band fidelity among all females increased 25.7% in the year following vaccination and culling, despite the social perturbation associated with removal of conspecifics. Herding behavior by stallions decreased 50.7% following treatment and culling ($P < 0.001$), while harem-tending behavior increased 195.0% ($P < 0.001$). The amount of available forage influenced harem-tending, reproductive, and agonistic behavior in the year following culling and treatment ($P < 0.04$). These changes reflected the expected nexus

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between a species with polygynous social structure and strong group fidelity and the large instantaneous change in population density and demography coincident with culling. Behavioral responses to such perturbation may be synergistic in reducing grazing pressure by decreasing energetically expensive competitive behaviors, but further investigation is needed to explicitly test this hypothesis.

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1. Introduction

Gregarious relationships can impart individual benefits such as decreased depredation, increased foraging efficiency, and increased fecundity (Pusey and Packer, 1997). When resources to support populations of social animals are limited and populations become locally overabundant, managers are faced with the daunting challenge of decreasing population size without disrupting core behavioral processes. For example, the limited contiguous habitat and finite resources found on public wildlands cannot sustain overabundant populations of large ungulates, and managers continuously seek innovative and publically-acceptable tools for managing these species (Powers et al., 2011). Historically, such populations have been reduced by culling, using either lethal methods such as hunting, or non-lethal methods such as capture and translocation. Limiting fecundity through the use of immunocontraceptives is becoming a more commonly considered tool for controlling wildlife abundance. However, these tools can be accompanied by physiological changes that may alter behavior and ultimately influence population dynamics in unforeseen ways (Ransom et al., 2014). The paucity of quantitative data on natural behavior of wild free-roaming fauna, especially pertaining to those treated with fertility control agents, impairs our ability to understand species' influences and roles in ecosystems and thus our ability to effectively manage populations.

Elk (*Cervus canadensis*) and feral horses (*Equus caballus*) are increasingly targeted for fertility control management in the United States and both species exhibit complex social behavior and polygynous mating systems. Whereas elk congregate seasonally into mating groups (Geist, 1982), feral horses form bands that persist year-round with distinct associations of individuals sometimes lasting a decade or more (Klingel, 1982). These bands are largely maintained by reproductive, herding, agonistic, and defensive behaviors initiated by the polygynous male in the band, as well as hierarchical relationships among females (Ransom and Cade, 2009). Culling can result in discrete changes to population density and demography, which could perturb social organization. Likewise, effective fertility control agents lead to discrete changes in presence of offspring in the population, and thus may influence social behavior.

Approximately 33,000 feral horses roam 13 million ha of public lands in the western United States and managers have historically relied on nonlethal culling through a process of capture, removal, and public adoption to regulate animal abundance (Garrott and Oli, 2013). This process is unsustainable because demand in the U.S. for feral horses as domestic stock is less than half the number of animals

removed, which has left as many horses in federally-subsidized pastures as persist in the wild. Several fertility control techniques have been investigated for use in feral horses, but most of these efforts resulted in tools that were publicly unacceptable, expensive to use, or impractical on a large scale. Among the most promising techniques are immunocontraceptive vaccines such as porcine zona pellicuda (PZP) and gonadotropin-releasing hormone (GnRH). These agents are relatively easy to apply, are reasonably efficacious, and are not expected to be accompanied by serious contraindications (Kirkpatrick et al., 2011).

Gonadotropin releasing hormone is a small neuropeptide that performs an obligatory role in mammalian reproduction. When combined with a potent adjuvant, the GnRH vaccine stimulates a persistent immune response resulting in prolonged antibody production against GnRH, the carrier protein, and the adjuvant (Miller et al., 2008). The most compelling hypothesis of vaccine effectiveness suggests that antibodies to GnRH likely induce transient infertility by binding to endogenous GnRH, thus preventing attachment to receptors on gonadotropes and suppression of pulsatile luteinizing hormone (LH) secretion (Molenaar et al., 1993). Gonadotropin releasing hormone antibody titers are correlated with suppression of the reproductive system and infertility in a variety of species (Fagerstone et al., 2010). As anti-GnRH antibodies decline over time, concentrations of available endogenous GnRH increase and treated animals usually regain fertility (Powers et al., 2011).

This immunocontraceptive vaccine, known by the trade name as GonaCon-B™, has been shown to provide multiple years of infertility in several wild ungulate species including horses (Killian et al., 2008; Gray et al., 2010), bison (*Bison bison*) (Miller et al., 2004), elk (Powers et al., 2011), and white-tailed deer (*Odocoileus virginianus*) (Gionfriddo et al., 2009). Given the physiological mechanism of action, GnRH immunocontraception has the potential to reduce fertility and suppress the reproductive behaviors typically associated with copulation; however, in GnRH-vaccinated elk, such behaviors were not entirely diminished likely due to incomplete suppression of the hypothalamic pituitary gonadal (HPG) axis (Powers et al., 2011). Similar to elk, feral horses are polyestrous and fertility control agents that do not suppress these social behaviors can lead to females exhibiting frequent reproductive behaviors that can cascade into altered behaviors from associated band members and nearby males (Nuñez et al., 2009; Ransom et al., 2010).

Rigorous quantitative investigation into the potential effects of GnRH treatment on feral horse behavior is missing from the assessment of this immunocontraceptive as a potential management tool. Such data are

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