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The effects of immunocontraception on harem fidelity in a feral horse (*Equus caballus*) population

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ABSTRACT

Feral horses on Shackleford Banks Island, North Carolina, are managed by the National Park Service in order to reduce their impact on the fragile barrier island ecosystem. Management techniques include removal of young horses and immunocontraception of many of the mares using Porcine Zona Pellucida immunocontraceptive. This immunocontraceptive reduces the number of horses that need to be physically removed from the island, but there is concern that the contraception may be influencing the social behavior of the contracepted mares. We investigated the effect of immunocontraception on harem stability by tracking the number of harem changes of each adult mare through the breeding season over two seasons. In both seasons the mares that had been treated with the immunocontraceptive changed harems significantly more than mares never treated (2007 $P = 0.037$ and 2008 $P = 0.016$) and visited significantly more harems (2007 $P = 0.021$ and 2008 $P = 0.011$). The number of years treated did not have a significant effect on the number of harem changes (2007 $P = 0.145$ and 2008 $P = 0.848$), nor did the number of years a mare had been off contraceptive once the contraceptive was discontinued (2007 $P = 0.443$ and 2008 $P = 0.826$). Additionally, there was no significant difference in harem changes between mares that were actively contracepted and mares that had been treated in the past but were not currently actively contracepted (2007 $P = 0.336$ and 2008 $P = 0.533$). These results indicate that the PZP immunocontraceptive has a significant effect on harem stability and that once a mare has been contracepted the behavioral effect of the contraceptive treatment may not be readily reversed.

1. Introduction

Feral horse populations are often considered to be a nuisance due to their competition with livestock and their effect on native habitats (Rubenstein, 2001). Although commonly associated with grassland habitats, feral horses also occur on barrier islands, where they have been shown to have significant effects on native flora and fauna (Turner, 1969). De Stoppelaire et al. (2004) found that feral horse grazing had a significant negative impact on dune formation and contributes to dune erosion. Overgrazing of marsh areas may result in a loss of important nursery habitat for many marine species (Levin et al., 2002). Due to the impact of feral horse populations on the environment, populations are often actively managed to reduce population size through a variety of strategies, including selective removals, adoption programs, and fertility control (Rubenstein, 2001).

Feral horses generally associate in harems or bands consisting of up to three adult males, a group of adult females,

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and their offspring (Linklater et al., 2000; Rubenstein, 1981, 1986). Although these social groups are generally stable (Klingel, 1975; Linklater et al., 2000) several studies have documented harem changes by adult females (Blumenshine et al., 2002; Rubenstein, 1981; Stevens, 1990). Harem stability has been found to positively correlate with yearly (Rubenstein, 1986) and lifetime reproductive success in females (Kaseda et al., 1995), possibly because mares that are more stable are able to devote more time to grazing and thus are in better condition to support a foal (Rubenstein, 1986). Females that change harems less frequently are more likely to reproduce and produce foals that survive to independence than mares that change harems more frequently (Rubenstein and Nuñez, 2009). Linklater et al. (1999) proposed that stable relationships between females and a harem male or group of males serve to reduce intraspecific aggression and the resultant reproductive costs. Altering harem stability may therefore alter overall reproductive rate, effective population size, and patterns of genetic diversity critical to maintaining long term stable populations. Thus, successful management of feral horse populations requires an understanding of how management strategies may alter social structure.

Population management through contraceptive use may minimize disturbance to social structure by preventing reproduction without altering group size or composition (Garrott and Taylor, 1990). Porcine Zona Pellucida (PZP) immunocontraception has been proposed as a contraceptive agent because it can be administered remotely through the use of darts, is relatively inexpensive, and has been shown to be safe and effective in many animal species (Barber and Fayrer-Hosken, 2000; Martinez and Harris, 2000). Immunocontraception with PZP is also temporary, lasting approximately two years in horses when conventional dosing schedules are used (Powell and Monfort, 2001), although treatment for over seven years may not be reversible (Kirkpatrick and Turner, 2002).

However, the results of studies that have assessed PZP impact on social behavior in feral horses are inconsistent. In a study of Assateague Island horses, no impact on social behavior was noted (Kirkpatrick et al., 1995). Other studies have found no effect on aggression initiated or received, activity budgets of mares, sexual behavior, or proximity to stallions (Powell, 1999; Powell and Monfort, 2001). In contrast, Nuñez et al. (2009) documented an increase in harem changes, number of harems mares associated with, and reproductive behaviors in treated mares. This study was conducted over a span of five weeks, included a limited number of mares, and occurred during the non-breeding season (Nuñez et al., 2009). Given the potential impact of increased rate of harem change on individual fitness, additional study is clearly necessary to determine if there is a significant effect of PZP immunocontraception on harem changes.

In this study we investigated the effect of PZP immunocontraception on harem stability of the feral horse population on Shackleford Banks, North Carolina, USA, during the course of two breeding seasons. We examined the number of harem changes each mare on the island made and the number of harems each mare visited during the course of the 2007 and 2008 breeding seasons. Every mare on the island was included in the analysis and data were collected over a period of several months each year. Given the previous work conducted by Nuñez et al. (2009), we hypothesized that contracepted mares would change harems significantly more often than control mares over both seasons and that contracepted mares would visit more harems than control mares. We also analyzed the effect of foaling status on harem changes, hypothesizing that mares that foaled during the survey year would change less than non-foaling mares.

We also attempted to relate the historical record of immunocontraception with the current patterns of harem changes. We examined the relationship between number of years contracepted, number of consecutive years contracepted, or number of years off contraception and harem changes. We predicted that harem changes would increase as the number of years contracepted increased and the number of consecutive years contracepted increased. Conversely, we predicted that the number of harem changes would decrease as the number of years off contraception increased. Finally, we examined the number of harem changes made by females that were actively contracepted in comparison to those that had been contracepted in the past, but were not currently contracepted. We predicted that actively contracepted mares would change harems more than mares with lapsed contraception.

2. Materials and methods

2.1. Study area

Shackleford Banks is a small barrier island located approximately 3 km off the coast of North Carolina, USA, in Cape Lookout National Seashore. The island is approximately 17 km long and 1 km wide with a variety of habitats including beach, swale, dunes, salt and freshwater marshes and maritime forest (Rubenstein, 1981). Individual horse bands are generally distributed along the entire island but individual harems occupy home ranges within a portion of the island. These home ranges can be grouped into far-east, mid-east, and western distributions. Each area contains at least one permanent water source, although digging may be necessary to access the water. Subjects in all areas of the island were observed for this study.

2.2. Study subjects

There are currently approximately 120 horses on the island. Most horses on the island are found in harems including one to two males and a group of mature females and their immature offspring. Several harems have an alpha stallion and a beta stallion. Over the course of the study, harem sizes ranged from a single male and a single female to two males, multiple females, and multiple offspring. Both sexes disperse from their natal harems as found in other feral horse populations (Feh, 1990). Territoriality has been reported on the island in the past (Rubenstein, 1981), but does not appear to exist currently. This change may be the result of reduced water sources in the eastern end of the island where territories were found. Harems and solitary stallions tend to be found within the same general area of the island from season to season and year to year. There is some movement between areas, especially by dispersing juveniles, but most adult horses settle into one area of the island. There are exceptions – during a particularly dry summer several harems shifted areas or expanded their home range in order to access a better water source and there is more overlap between harems occupying the mid-east and far-east areas than between those in the mid-east and the west.

The minimum population of Shackleford horses is fixed by federal law at 100 horses (Prioli, 2007), and the National Park Service limits the population to approximately 130 individuals to reduce the potential for damage to the island ecosystem. The immunocontraception program was initiated in 2000 to reduce population size and control population growth (Nuñez et al., 2009). The contraceptive is administered by dart gun by the National Park Service between February and April every year. Each dose contains 100 μg of PZP mixed with 0.5 cm^3 of either Freund's Complete Adjuvant, Modified, *Mycobacterium butyricum* (Calbiochem, Gibbstown, NJ, USA, #344289) for initial doses, or Freund's Incomplete Adjuvant (Sigma, St. Louis, MO, USA, #F5506) for subsequent doses (S. Stuska, personal communication; Nuñez et al., 2009). Booster doses are administered at least 14 days after the initial dose. At the initiation of the program eight mares were chosen as controls, chosen from eight distinct genetic lineages present on the island. These controls have never been contracepted. One additional control was added in 2007 in order to increase the age variation in controls and is included in the data analyzed for 2007, but died before the breeding season in 2008.

We observed harem affiliations for every mare on the island. Only mares that had dispersed from their natal harems were included in the analysis: nine controls and 55 contracepted mares in 2007 and eight control mares and 57 contracepted mares in 2008. The contracepted mares consisted of any mare that had ever been treated with the contraceptive, regardless of whether they had been treated in the previous year. We included all mares ever contracepted as there is some evidence that the contraceptive effect may last longer than one year (Powell and Monfort, 2001) and it is important to determine if contraception at any point changes the mare's subsequent behavior.

2.3. Behavioral sampling

The study was conducted by multiple observers supervised and trained by the primary investigator (J M). All observations were collected during the breeding season. Observations were collected between May 22nd, 2007 and July 29th, 2007 and between May 22nd, 2008 and August 12th, 2008, totaling 2965 total sightings in 2007 and 2985 total sightings in 2008. A sighting was defined as an independent positive identification of a mare and her harem association. Each observer recorded initial sightings upon identifying individuals. Unless a mare changed harems more than 20 min after the initial sighting no additional sightings were recorded of the harem by that observer unless the harem was independently identified at a later point in the day. If two observers identified the same individuals within 20 min only one identification was included in the sightings count. Harem changes were recorded regardless of their timing during the observation session. Individual horses were identified by freeze brand, distinctive markings on the face and body, color, and sex.

Harems were located an average of five times a week during 2007 and approximately four times a week during 2008. Each mare was sighted an average of 46.3 times in 2007 (S.E. 1.70) and 45.9 times in 2008 (S.E. 1.64), or approximately every 1.2 days (2007) and every 1.6 days (2008). After examining the standardized Z score, no individuals were found to be outliers, and there was no correlation between the number of sightings and harem changes for either year (2007 $P = 1.82$ and 2008 $P = 0.502$). Each time a harem was located the harem members were all individually identified and the composition was recorded along with the GPS location of the harem. The number of harem changes for each mare on the island was quantified as a change from one harem to another over successive sightings. All sightings from all observers were compiled for each season and each move from one harem to another was counted. Absence from a harem without a sighting in a different harem was not counted as a harem change as in some rare cases mares were found without a harem stallion. The number of harems a mare visited was quantified as the number of harems a mare was affiliated with over a given season.

2.4. Statistical analysis

We analyzed the effect of contraception on the mean number of harem changes per individual per season using Mann–Whitney U tests. The Mann–Whitney U test was selected given the non-normality of the data and the large difference in sample size between the control (nine in 2007, eight in 2008) and contracepted (55 in both years) mares, which may cause problems when using t-tests (Zar, 1999). One-tailed tests were used as we predicted that contracepted mares would change harems significantly more than control mares given the previous work by Nuñez et al. (2009). Effect size provides a measure of the strength of the relationship between the variables and was calculated using G-power (Faul et al., 2007) for a one-tailed t-test, which provides a reasonably equivalent estimate for the Mann–Whitney U analysis (Zar, 1999). Data were analyzed independently for each year and statistical outliers (one per year) were eliminated from the analysis. In this study both statistical outliers were contracepted mares that changed harems repeatedly over the season. Eliminating the outlier in each year made the analysis more conservative.

We examined the effect of age on harem changes using nonparametric correlation (Spearman's rho) between age on June 1st of the survey year and number of harem changes during that survey season. We ran Mann–Whitney U tests to determine if the average age differed between control and contracepted females. We also ran Kruskal–Wallis tests to determine if mares that foaled during a given survey year changed harems less than mares that did not foal based on their contraceptive status. All mares that foaled during the survey year (not just during the data collection season) were included as mares that foaled even if the foal did not survive. The mares eliminated as statistical outliers for earlier analyses were also eliminated from the age and foaling analyses.

To investigate the impact of historical contraception patterns on current behavior, we analyzed the effect of total number of years contracepted, number of years contracepted consecutively with the survey year, total number of years ever consecutively contracepted, and number of years off contraception prior to the survey year on harem changes using Kruskal–Wallis tests. Our assessment of contracepted status in a given year was based on National Park Service records, and included only contraception attempts deemed successful (solid hit with the dart and immunocontraceptive solution ejected from the dart) were included. We analyzed the effect of active versus lapsed contraception on harem changes using Mann–Whitney *U* tests. Mares were considered to be actively contracepted if contraception had been administered in the past two years (Powell and Monfort, 2001). Again, data were analyzed independently for each year and statistical outliers were eliminated from the analysis. All analyses were conducted in SPSS 15 (SPSS Inc., 2006).

3. Results

3.1. Immunocontraception and harem changes

During 2007, there were nine controls and 55 contracepted mares; of the contracepted mares 25 received PZP in the previous year and 20 had not. Sixty-six percent of mares changed harems at least once over the season, with most changing harems multiple times. One individual mare changed harems 26 times over the course of the field season (the outlier in 2007 – a contracepted mare). Additionally, 70.9% of contracepted mares (39 of 55) changed harems at least once while 33.3% of control mares (three of nine) changed harems. Contracepted mares changed harems significantly more than control mares (Mann–Whitney $U = 157.00$, one-tailed $P = 0.0415$, effect size $(d) = 0.61$). The mean number of harem changes for contracepted mares was 3.62 ± 0.606 S.E., while the mean number of harem changes for uncontracepted mares was only 1.44 ± 0.766 S.E. (Fig. 1). Contracepted mares also visited more harems than control mares (Mann–Whitney $U = 145.5$, one-tailed $P = 0.021$, effect size $(d) = 0.80$). The mean number of harems visited for contracepted mares was 2.73 ± 0.213 S.E., while the mean number of harems visited for control mares was 1.67 ± 0.333 S.E.

During 2008, there were eight controls and 55 contracepted mares; 20 contracepted mares had received PZP in the previous year and 37 had not. Seventy-three percent of mares changed harem at least once, with a maximum of 27 harem changes (the outlier for 2008 – a different contracepted mare). In 2008, 77.2% of contracepted mares (44 of 57) changed harems at least once while only 50% of control mares (four of eight) changed harems. Again, contracepted mares changed harems significantly more frequently than control mares (Mann–Whitney $u = 124.5$, one-tailed $P = 0.0205$, effect size $(d) = 0.92$). In 2008, the mean number of harem changes for contracepted mares

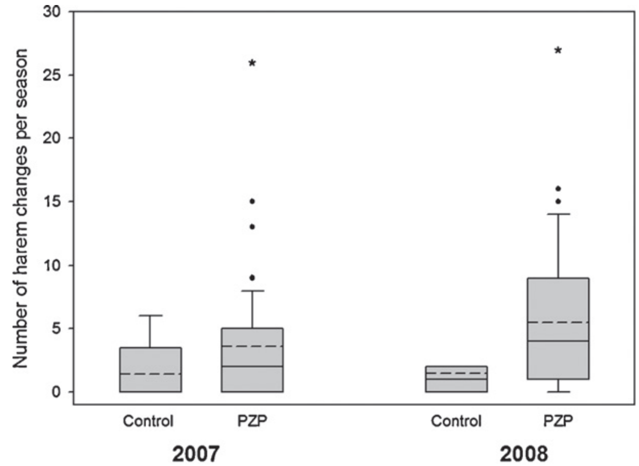

Fig. 1. Box plot showing the number of harem changes by contraceptive status for both 2007 and 2008 with median (solid line), mean (dashed line), and statistical outlier (asterisk). The statistical outlier is presented, but not included in analysis.

was 5.47 ± 0.758 S.E., while the mean number of harem changes for control mares was only 1.50 ± 0.732 S.E. (Fig. 1). Contracepted mares visited more harems that control mares (Mann–Whitney $U = 115$, one-tailed $P = 0.011$, effect size $(d) = 1.10$). The mean number of harems visited for contracepted mares was 3.05 ± 0.222 S.E., while the mean number of harems visited for control mares was 1.63 ± 0.263 S.E.

3.2. Age and harem changes

Age of the mare was not found to correlate with harem changes in either year (2007 rho = −0.073 (61), $P = 0.569$, 2008 rho = −0.023(62), $P = 0.854$). Additionally, average age was not significantly different between contracepted mares and control mares (2007 Mann–Whitney $U = 200.5$, $P = 0.403$, 2008 Mann–Whitney $U = 139$, $P = 0.084$).

3.3. Foaling and harem changes

In 2007, six control mares foaled and four non-control mares foaled; two non-controls had been off PZP for at least a year while two others had been contracepted the previous year. In 2008, seven control mares foaled and eight non-control mares foaled; again two mares contracepted the previous year foaled. In 2007, the 92% of treated mares did not foal while in 2008 90% of treated mares did not foal. There was a significant difference in the number of harem changes between mares that foaled and those that did not foal in 2008 (Mann–Whitney $U = 240.5$, $P = 0.042$) and a borderline significant difference in 2007 (Mann–Whitney $U = 165.0$, $P = 0.054$). In both cases mares with a foal changed harems less than mares without a foal. There was no significant difference in the number of harem changes between mares that were previously contracepted and foaled, mares that were controls and foaled, and mares that did not foal (Kruskal–Wallis 2007 $P = 0.120$, df = 2; 2008 $P = 0.112$, df = 2), but in both years mares that had previously been contracepted and foaled changed harems less than contracepted mares without foals and more that control mares with foals.

3.4. Prevalence of harem changing

The distribution of harem changes each season significantly differed from the Poisson distribution (2007: Chi-square = 269.11, df = 10, $P < 0.001$; 2008: Chi-square = 761.15, df = 10, $P < 0.001$) suggesting that harem changes are not random. In general, there were more mares at the extremes and fewer mares in the center of the distribution than expected in a Poisson distribution. Prior to the immunocontraception program only 10.8% of mares changed harems in the same study area (Rubenstein, 1981) as opposed to the 66% and 73% found over the two seasons of this study. This difference was significant for both years (2007: Chi-square = 316.293, df = 1, $P < 0.001$; 2008: Chi-square = 401.599, df = 1, $P < 0.001$). In 2007, 94% of harems experienced at least one mare changing into or out of the harem and in 2008 97% of harems were affected by the harem changes.

3.5. Historical PZP treatment and harem changes

The number of years treated with PZP did not have a significant effect on the number of harem changes (Kruskal–Wallis 2007 $P = 0.199$, df = 6; 2008 $P = 0.871$, df = 7), nor did the number of years a mare had been off contraceptive after it had been discontinued (Kruskal–Wallis 2007 $P = 0.310$, df = 4; 2008 $P = 0.823$, df = 5). The number of years a mare had been treated consecutively with the survey year did not have a significant effect (Kruskal–Wallis 2007 $P = 0.273$, df = 7; 2008 $P = 0.093$, df = 4), nor did the maximum number of years a mare had ever been consecutively treated (Kruskal–Wallis 2007 $P = 0.782$, df = 6; 2008 $P = 0.889$, df = 6). There was no significant difference in harem changes between mares that were actively contracepted and mares that had been contracepted in the past but were not currently actively contracepted (2007 Mann–Whitney $U = 275.0$, $P = 0.196$, 2008 Mann–Whitney $U = 365.0$, $P = 0.751$).

4. Discussion

It is important in any management program to reduce the impacts of the management on the natural behavior of the population, though the importance of preserving behavior is often overlooked (Clemmons and Buchholz, 1997). In a highly social species such as feral horses it is critical to ensure that management strategies do not negatively impact social behavior. The results of this study indicate that the PZP immunocontraceptive used to control population numbers on Shackleford Banks Island has a significant negative effect on harem stability and that this behavioral effect is more persistent than the physiological contraceptive effect documented in previous studies (Powell and Monfort, 2001). This study demonstrates that the negative effect of the PZP immunocontraception on harem stability during the non-breeding season (Nuñez et al., 2009) was also present in the breeding season and that age was not related to number of harem changes in a given season. The significant increase in the historic rate of harem changes (from approximately 10% to approximately 66 and 73%) indicates that the overall rate of harem changes has increased since the immunocontraceptive program was initiated. Additionally, the high percentage of harems affected by harem changes indicates that the change in stable social structure after PZP immunocontraception affects the entire population, not just the mares contracepted.

Although the control sample size in this study was necessarily small due to management concerns, the replication of these results over two breeding seasons increases our confidence in the significance of differences in harem changes between contracepted and control mares. Given that mares stayed in the same general area, they frequently revisited the same harem several times during the season. The average number of harems visited for all mares was 2.58 in 2007 and 2.88 in 2008. Contracepted mares visited more harems than control mares in both years. It is important to note that some mares changed harems several times over the course of a week or even a day. High temporal resolution is critical to insure that these rapid harem changes between small numbers of harems are documented.

4.1. Impacts of historical contraceptive treatment

The fact that the number of harem changes did not differ among mares contracepted for different numbers of years, or different numbers of consecutive years, suggests that any exposure to PZP contraception may alter female behavior in fundamental ways. Additional years of contraception did not result in a higher number of harem changes, indicating that contracepting for multiple years does not decrease social stability further. However, increasing the number of years between contraception did not mitigate the behavioral effect of the contraception as expected. Surprisingly, mares that were not currently contracepted but had been in the past did not change harems less than mares that were actively contracepted. These analyses indicate that contraception schedule does not seem to mitigate the behavioral effects of the contraception and that the behavioral effects of the PZP contraception may persist long after the contraceptive should no longer be physiologically effective.

4.2. Influence of foals on harem fidelity

As seen in the non-breeding season (Nuñez et al., 2009), mares that had foals changed harems less than mares without a foal, regardless of their contraceptive status. The presence of a foal may increase mare fidelity. Unfortunately, it is difficult to separate the effect of the contraceptive itself from the result of the contraceptive – a lack of foals. If the presence of a foal is a driver of harem fidelity all contraceptive strategies may reduce social stability. Although not significantly different, the pattern of harem changes suggests that previously contracepted mares with foals may change more than controls with foals, but less than contracepted mares without foals suggesting that the contraceptive may have an effect beyond the presence of a foal. The failure to find a significant difference in this comparison may be due to low sample size. Further studies should be conducted with higher sample size to determine if contracepted mares with foals change harems at the same rate as control mares with foals.

It is possible that foaling returns mares to pre-contraceptive behavior – the sample size of this study was simply too low to conclusively answer this question. Relatively few mares that had been previously contracepted, but were not currently contracepted, foaled in either year – two out of 30 in 2007 and six out of 37 in 2008. Further studies should be conducted to determine if contracepted mares cease changing harems the season after they are reproductively successful or if they continue to change harems at a higher rate than mares that are never treated.

4.3. *Potential motivations for harem infidelity*

While it is clear that PZP immunocontraception causes a decrease in harem fidelity in this population regardless of season, it is unclear if this decrease is due to male or female choice. Males have been shown to discriminate between females based on female reproductive success in many taxa (Berglund et al., 1986; Berven, 1981; Johnson and Hubbell, 1984; Jones et al., 2001; Szykman et al., 2001; Verrell, 1985). This male choice may result in males defending reproductively successful mares (as evidenced by their foals) more than contracepted mares, allowing contracepted mares to change harems more often due to reduced male attentiveness. Previous studies found increased herding of mares with foals, but no difference in harem tending behaviors between currently contracepted mares and controls (Ransom et al., 2010). Alternatively, continuous cycling may lead to increased breeding attempts (Ransom et al., 2010) and male harassment of contracepted females. Contracepted females may elect to change harems more frequently to escape harassment or in an attempt to become pregnant. Future work aimed at distinguishing between male and female choice would be of particular interest.

4.4. *Fitness impacts of decreased harem stability*

Finally, the pervasive pattern of decreased harem stability may affect individual fitness of both males and females. In feral horses the breeding season corresponds to the foaling season (McCort, 1984) and thus a decrease in harem stability may lead to decreased grazing time while caloric demands on lactating mares are highest (Pagan, 1998; Pilliner, 1999) and decreased body condition even among mares that do not change harems. Ransom et al. (2010) found no difference in grazing time between treatment groups, but did not consider the overall effect of decreased harem stability on grazing. With decreased social stability, males may be required to spend more time guarding their harem to prevent harem changes. This increase in time spend guarding harems may lead to reduced time grazing and result in lowered body condition for the harem stallions. Future work will test if body condition of males or females has decreased since the implementation of the immunocontraception program.

4.5. *Management implications*

The contraception of the majority of adult females on the island may have substantially changed the social structure of the population, and it is unclear if contracepted mares will ever return to pre-contraception social stability. Immunocontraception using PZP offers many potential benefits, but managers should also consider the potential impacts PZP may have on social structure and stability. One of the key benefits of PZP immunocontraception is the temporary nature of the contraceptive affect. However, even if mares can be physiologically restored to reproductive condition; their continuing propensity to move may reduce their subsequent fitness and complicate management. The persistent behavioral effects are not reduced by manipulating the number of years treated with PZP, so reducing these behavioral effects may not be possible.

Given that PZP immunocontraceptive is administered to a wide variety of species including deer, African elephants, feral water buffalo, feral burros, elk and more than 95 species of zoo animals (ZooMontana, 2000), it is critical to further examine the behavioral effects the contraception may have on other species. Although immunocontraception does not have some of the potential physiological effects of steroidal contraceptives and while behavioral effects may vary with different social systems present in different species, this study indicates that social behavior can be changed by PZP immunocontraception. If, as is known in horses, social behavior affects reproductive success, population management may be complicated by lingering changes in social dynamics. Managers of other species treated with PZP should be cautious in assuming that PZP immunocontraception ameliorates the behavioral effects of other types of contraception.

5. Conclusions

This study, combined with previous work, demonstrates that there is a significant effect of PZP contraception on behavior in feral horses. Contracepted mares changed harems significantly more often than control mares. Further, a high percentage of mares change harems over the course of each season, indicating that this change is affecting the entire population. The duration of contraception does not have an effect on harem changes, nor does the duration of time off contraception reduce harem changes. Mare behavior is altered after contraception and this alteration appears to be long-lived. Given the pervasive behavioral effect of the PZP immunocontraception and the duration of this behavioral effect, it is especially important to investigate the potential costs of the reduction in harem stability to both sexes regardless of the direct effect of the contraceptive.

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