

THESIS

UNDERSTANDING THE INFLUENCES
OF IMMUNOCONTRACEPTION ON EQUIDS
THROUGH COMPETING MODELS OF BEHAVIOR

Submitted by

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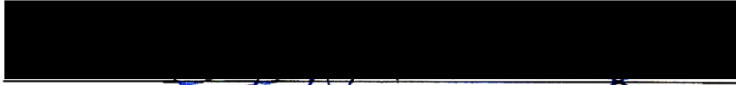
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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR
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ABSTRACT OF THESIS

UNDERSTANDING THE INFLUENCES OF IMMUNOCONTRACEPTION ON EQUIDS THROUGH COMPETING MODELS OF BEHAVIOR

The rapid increase in human populations over the last several decades has lead to shrinking habitats and limited resources for many large vertebrates around the world. In response, managers seek effective tools for limiting population growth in some species, yet little is known about impacts of fertility control on the behavioral ecology of wild, free-roaming animals. Feral horses (*Equus caballus*) in the western United States are ideal candidates for contraceptive management due to broad scale federal protection, high fecundity, and finite public land allocated for them. The complex mating system of feral horses relies on behavioral manipulation of females by a polygynous male and a balance between reproductive and maintenance behaviors to promote fitness gains. I investigated influences of the immunocontraceptive porcine zona pellucida (PZP) on individual and social behavior within bands of feral horses in three discrete populations.

A candidate set of 26 hierarchical mixed effect linear models was analyzed by restricted maximum likelihood, using treatment given discrete population as a random effect. Treated and control females in the most fecund cohort (6–14 years old) and the less fecund older cohort (≥ 15 years old) allocated their behavioral time budgets

differently, but females in the youngest cohort spent time equitably. Stallions herded control mares in the 6–14-year group more than contracepted mares with treatment being the most supported effect, but presence of a dependent foal resulted in less herding by stallions and contributed strongly to the model. Contracepted mares received more reproductive behaviors from stallions than control mares in the 6–14-year cohort. No differences were detected in herding or reproductive behaviors in the least fecund groups. Stallions showed no differences in harem tending or agonism toward treatment groups of any age cohort for harem tending or agonism; however, stallions tended high body condition females more often. Stallions maintained closer spatial relationships with 2–5 year-old treated females than with control females of the same age while the group was feeding (at its most dispersed structure), but there were no differences while the bands were resting or in locomotion. There were no spatial differences between stallions and females detected by treatment in the other age cohorts, although several well-supported models found spatial relationships varied significantly by band fidelity and band size.

Direct effects of PZP treatment on the behavior of feral horses were minimal and most differences detected between treatment groups were attributed to the secondary effects of body condition, band fidelity, and foal presence. Though statistical support was found for some differences in behavior between treatment groups, these appeared to have little biological meaning in the short term. The population-scale magnitude of behavioral change attributed to fertility control may vary by vaccination management strategy (proportion of females treated) and ecology of the population because individual behavior

can influence social behavior in conspecifics. PZP is a promising alternative to traditional hormone-based contraceptives, leading to few acute behavioral modifications in female horses.

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DEDICATION



Francis J. Singer

September 29, 1949 – September 21, 2005

This thesis is dedicated to the memory of Dr. Francis J. Singer, a dearly missed mentor, inspiring ecologist, colleague, and friend. His passion for ungulate ecology, love of nature, and kind actions fostered my career path and led to my academic success. He contributed 30 years of science to understanding the ecology of bighorn sheep, elk, bison, and horses and it is through his efforts that the feral horse project has succeeded and continues to develop. I regret that I cannot share this milestone with him and I dearly hope that this thesis has fulfilled his vision. I am humbly grateful to have had the honor of continuing his work.

TABLE OF CONTENTS

ABSTRACT OF THESIS	iii
ACKNOWLEDGMENTS	vi
DEDICATION	viii
TABLE OF CONTENTS	ix
LIST OF TABLES	xi
LIST OF FIGURES	xiv
INTRODUCTION	1
METHODS	5
Study Areas	5
Behavior	7
Covariates	10
Analyses	11
RESULTS	14
Time Budgets	15
Social Interactions	21
Herding Behavior	21

Reproductive Behavior	24
Harem Tending Behavior.....	25
Agonistic Behavior	26
Spatial Relationships.....	27
DISCUSSION	31
CONCLUSION.....	38
REFERENCES	40
APPENDIX A: Study Area Locations and Population Structures.....	47
APPENDIX B: Model Selection.....	54
BEHAVIOR GLOSSARY	60

LIST OF TABLES

Table 1. Candidate model set for analyses of feral horse behavior.....	13
Table 2. Climate conditions during 2003–2006 behavioral observations at Little Book Cliffs Wild Horse Range (LBC), McCullough Peaks Herd Management Area (MCP), and Pryor Mountain Wild Horse Range (PRY).....	15
Table 3. Hierarchical linear mixed model estimates for the difference in means of compositional time budget behaviors for 2- to 5-year-old female feral horses ($n=124$) at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.	17
Table 4. Hierarchical linear mixed model estimates for the difference in means of compositional time budget behaviors for 6- to 14-year-old female feral horses ($n=153$) at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.	18
Table 5. Hierarchical linear mixed model estimates for the difference in means of compositional time budget behaviors for ≥ 15 -year-old female feral horses ($n=40$) at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.	20

Table 6. Hierarchical linear mixed model estimates of the difference in means, by female age cohort, for each fixed effect in the most supported models of stallion-initiated social behavior at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.....	23
Table 7. Analysis of Variance results for the difference in mean distance for each fixed effect in the most supported models of spatial relationships of male-female feral horse pairs at Little Book Cliffs, McCullough Peaks, and Pryor Mountain, 2003–2006, while bands were feeding.	28
Table 8. Analysis of Variance results for the difference in mean distance for each fixed effect in the most supported models of spatial relationships of male-female feral horse pairs at Little Book Cliffs, McCullough Peaks, and Pryor Mountain, 2003–2006, while bands were resting.....	29
Table 9. Analysis of Variance results for the difference in mean distance for each fixed effect in the most supported models of spatial relationships of male-female feral horse pairs at Little Book Cliffs, McCullough Peaks, and Pryor Mountain, 2003–2006, while bands were in locomotion.	31
Appendix A Table 1. Little Book Cliffs Wild Horse Range feral horse population composition from 2003–2006.....	49
Appendix A Table 2. McCullough Peaks Herd Management Area feral horse population composition from 2003–2006.....	51

Appendix A Table 3. Pryor Mountain Wild Horse Range feral horse population composition during 2003-2006.....	53
Appendix B Table 1. The four best fit models in each age cohort for individual daylight time budget behaviors.....	55
Appendix B Table 2. Compositional model selection for each age group using aggregated AIC _c scores.....	57
Appendix B Table 3. The four best fit models in each age group for stallion behavior directed toward females.....	57
Appendix B Table 4. The 4 best fit models in each age group for stallion spatial relationship (mean annual distance) to females while bands were in feeding (SF), resting (RE), and in locomotion (LO).....	59

LIST OF FIGURES

Figure 1. Rate of feral horse parturition as a function of control female age at the time of conception for the Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range populations, 2003–2006 ...	14
Figure 2. Hierarchical linear mixed model estimates for daylight time allocation of female feral horse behaviors in the 2- to 5-year-old (Model 1), 6- to 14-year-old (Model 4), and ≥ 15 year-old (Model 19) cohorts at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.....	16
Figure 3. Least squares estimates of resting behavior rates for 6–14-year-old female feral horses ($n=142$) in hierarchical linear mixed model 15, differentiating between resident and transient females and those with and without a dependent foal.	19
Figure 4. Hierarchical linear mixed model 19 for feeding (A) and resting (B) behavior in ≥ 15 -year- old control and treated female feral horses at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.	21
Figure 5. Herding behavior rate (times/hour) detected at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse	

Range, 2003–2006, as a function of the average distance maintained between stallion-female pairs.....	22
---	----

Figure 6. Hierarchical mixed model estimates of herding (Model 22), reproductive (Model 1), harem tending (Model 4), and agonism (Model 1) behaviors for 6- to 14-year-old control and treated female feral horses at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.....	24
--	----

Appendix A Figure 1. Location of the Little Book Cliffs Wild Horse Range and study area boundaries.	48
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Appendix A Figure 2. Location of the McCullough Peaks Herd Management Area and study area boundaries.....	50
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Appendix A Figure 3. Location of the Pryor Mountain Wild Horse Range and study area boundaries.	52
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UNDERSTANDING THE INFLUENCES OF IMMUNOCONTRACEPTION ON EQUIDS THROUGH COMPETING MODELS OF BEHAVIOR

INTRODUCTION

The size and distribution of human populations has rapidly increased over the last several decades, leading to shrinking habitats and limited resources for many large vertebrates around the world. Managers seek effective tools for limiting population growth in some species, yet little is known about impacts of fertility control on the behavioral ecology of wild, free-roaming animals. Understanding animal behavior can be an important tool in addressing a species' influences and roles in an ecosystem and can lead to better management and conservation practices (Sutherland 1998, Buchholz 2007). The ethical considerations of potentially altering animal behavior and social structure through the use of fertility control agents on free-roaming wildlife are also a growing concern among managers and the public (Nettles 1997; Asa et al 2005; Porton 2005).

Many wild ungulate species have complex mating systems that rely on ethological hierarchies within family groups, active recruitment and defensive behaviors by polygynous males, and resource driven behavioral patterns that may be unknowingly manipulated by the use of fertility control agents. Contraception of females has the

potential to induce cessation or repetitive estrous leading to abnormal reproductive behavior, changes in agonistic behaviors, artificial loss or gain in hierarchical structures of social groups, and degradation of pair-bonds and socialization due to absence of young animals (McCort 1979, McShea 1997, Asa et al. 2005, Munson et al. 2005, Penfold et al. 2005). Additionally, when individuals allocate more time to reproductive and social behaviors, less time is available for critical feeding and maintenance behaviors, potentially leading to long-term concerns for animal health and lifetime fitness.

Traditional fertility control agents have largely consisted of hormone-based contraceptives, and while being effective at limiting fertility, some have also produced considerable behavioral changes in the species receiving them. These modifications take a diverse array of expressions. Poiani et al. (2002) contracepted grey kangaroos (*Macropus fuliginosus*) with levonorgestrel and detected a change in social affiliation leading to a male preference for association with uncontracepted females; whereas, Ji et al. (2000) found an opposite trend in brushtail possums (*Trichosurus vulpecula*) treated with synthetic progestin norgestomet, and frequency of males increased near contracepted females. Variations in agonistic expression related to fertility control have also been diverse: hamadryas baboons (*Papio hamadryas*) exhibited a decrease in agonism when treated with a synthetic progestin (Portugal and Asa 1995) whereas stump-tailed macaques (*Macaca arctoides*) exhibited an increase in agonism when treated with a synthetic progestin (Linn and Steklis 1990). Penfold et al. (2005) supported this range of behavioral modification and found considerable variation in the agonistic expressions among various species treated with progestins and similar hormones. The range of behavioral changes attributed to hormone-based contraception varies by agent and

species, and any given expression may have considerable implications for species characterized by complex social structure and long-term family groups.

Large populations of ungulates (white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), and feral horses (*Equus caballus*)) are specifically targeted for fertility control management in the United States. Feral horses exhibit the Type I mating system found in the family Equidae, which is characterized by family groups (bands) of females and young, each with a single polygynous male (Klingel 1975; Rubenstein 1989). Such social groups are largely maintained by a suite of behaviors consisting of reproductive, herding, agonistic, and defensive expressions initiated by the polygynous male in the group, as well as hierarchical dominance relationships among females (Feist and McCullough 1976, Houpt et al. 1978, Klimov 1988, Pickeral et al. 1993, Linklater et al. 1999). With such complex structure, artificial changes to behavior may have far-reaching implications to both the treated individual and other members of the family group, as well as the social dynamics of the entire herd. An ideal fertility control agent for free-roaming populations of such animals would have little influence on behavior, and the immunocontraceptive porcine zona pellucida (PZP) is a proposed candidate.

PZP acts as a vaccine against pregnancy by stimulating the production of zona pellucida antibodies in female mammals (Liu et al. 1989). These antibodies provide a barrier that prevents sperm from binding to the surface of an ovum and results in limited penetration of the zona pellucida and subsequent limited pregnancy in many taxa (Kirkpatrick and Turner 1991; Kirkpatrick et al. 1996). Unlike most conventional contraceptives, this immunocontraceptive does not affect ovarian function of the inoculated female when used for up to 3 years; however, additional years of treatment has

been reported to decrease ovarian function in horses (Kirkpatrick et al. 1992, 1995). Because ovarian function remains normal for at least the 3-year treatment period and artificial hormones have not been administered, PZP is not believed to have a direct effect on the natural behavior of the animal. However, in polyestrous species such as horses, frequently occurring estrous cycles in an individual may elicit excess reproductive behaviors by both the cycling female and the dominant male in the group. Female feral horses may exhibit estrous behavior during both ovulatory and anovulatory phases of ovarian follicular development, which is thought to facilitate social structure since family groups remain together year-round (Crowell-Davis 2007).

PZP has been investigated for safety and efficacy (Liu 1989, Kirkpatrick et al. 1996, Kirkpatrick and Turner 2002). Many potential physiological side-effects of PZP treatment have also been investigated in domestic and feral equids (Kirkpatrick et al. 1992, 1995; Kirkpatrick and Turner 2003; Roelle and Ransom 2009); however, it remains unclear how PZP treatment influences the behavior of feral, free-roaming horses. Preliminary studies have been conducted on the behavioral effects of PZP on feral horses inhabiting barrier islands (Powell 1999, 2000; Rogers 2001) though concern has been expressed by managers regarding population and behavioral differences that may exist between small island populations and larger, wide-ranging populations in the western United States. I investigated influences of PZP immunocontraception on the behavior of feral horses in three discrete free-roaming populations. My objective was to quantify effects of immunocontraception on time budgets of individuals, and social interactions and spatial relationships within family groups, differentiating between control females and effectively contracepted females.

METHODS

Study Areas

Feral horses occupy a wide variety of habitats in the western United States. Three populations were chosen for this study: Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range. These populations use a mosaic of habitats, including desert, sage steppe, and montane environments typical of horse ranges in the western U.S. A small number of unimproved roads traversed these areas, but the majority of land at all three locations was designated as Wilderness Study Area and closed to motorized vehicles throughout the period of this study. All populations experienced management removals during this study. Hansen and Mosley (2000) reported no changes in feeding or reproductive behavior and no effect on fecundity following such removals. The number of immunocontracepted females in each population varied by year (Appendix A) and was determined by local managers.

Little Book Cliffs is located in Mesa County, Colorado, about 13 km northeast of Grand Junction and consists of 14,614 ha of dynamic terrain, with sloping plateaus, sagebrush parks, steep shale and sandstone cliffs, and 4 major canyon systems (Appendix A figure 1). The sagebrush parks are dominated by sagebrush (*Artemisia tridentata*), western wheatgrass (*Pascopyrum smithii*), Indian rice grass (*Oryzopsis hymenoides*), and blue wild rye (*Elymus glaucus*), intermixed with dense stands of Colorado piñon (*Pinus edulis*), and Utah juniper (*Juniperus osteosperma*). Annual rainfall on this range is 250–356 mm, and elevations range from 1,500 m to 2,250 m. The herd varied from 120 to 204 horses during this study and was distributed across the entire area in bands of 4.45 ± 0.16 horses (mean \pm SE, range= 2–9) (Appendix A table 1). Managers removed 68

horses from the range in 2004, but none were members of the focal bands used in this study.

McCullough Peaks is located in Park County, Wyoming, 32 km east of the town of Cody (Appendix A figure 2). It consists of 44,440 ha of predominantly flat, open sagebrush park, with rugged badlands along the western edge of the range. Prevalent vegetation includes sagebrush (*Artemisia tridentata*), Gardner's saltbush (*Atriplex gardneri*), greasewood (*Sarcobatus* sp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Pascopyrum smithii*), and blue grama, (*Bouteloua gracilis*). Annual rainfall of only 127–229 mm supports small ephemeral streams and associated stands of cottonwood (*Populus* sp.) and willow (*Salix* spp.). Elevations range from 1,200 m in the lowlands to 1,964 m at the summit of McCullough Peaks. The population varied from 112 to 495 horses during this study and was distributed across the entire area in bands of 8.01 ± 0.38 horses (range = 2–19) (Appendix A table 2). One focal band in the study included two equally dominant males, an atypical band structure that has been previously reported in feral horse populations with relatively large band sizes (Denniston 1979, Miller 1979, McCort 1984). Linklater et al. (1999) found the presence of multiple band stallions did not influence females' time spent feeding, resting, or in locomotion, but the study did not address social behaviors. In October 2004, managers removed 379 animals from the population. Due to management need, 1-year-old females, and 1- and 2-year-old males were removed from the focal bands used in this study, but all reproductive animals in these bands were captured and released as intact family units.

Pryor Mountain is located 21 km north of Lovell, Wyoming, and lies within northern Bighorn County, Wyoming, and southeastern Carbon County, Montana

(Appendix A figure 3). The range includes U.S. Bureau of Land Management land, portions of Custer National Forest and Bighorn Canyon National Recreation Area, and private lands, and consists of 16,046 ha of lowland desert, foothill slopes, forested montane slopes, steep canyons, and grassy plateaus. Vegetation types vary greatly from lower to higher elevations of the range with lower elevations dominated by sagebrush (*Artemisia tridentata*) and rubber rabbitbrush (*Chrysothamnus nauseosus*), mid-elevations dominated by curl-leaf mountain mahogany (*Cercocarpus ledifolius*), Utah juniper (*Juniperus osteosperma*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and blue grama (*Bouteloua gracilis*), and high elevations dominated by limber pine (*Pinus flexilis*), subalpine fir (*Abies lasiocarpa*), and alpine bluegrass (*Poa alpinum*). The elevation of Pryor Mountain ranges from 1,190 m to 2,625 m, with annual rainfall ranging from 130 mm in the arid lowlands to over 500 mm in the more mesic montane elevations. The population ranged from 142 to 168 horses during this study and most horses migrated from lower and mid-elevations in winter to high elevations in summer (Appendix A table 3). Horses at this site lived in bands of 4.16 ± 0.17 horses (range = 2–11). Small, targeted, individual removals of horses occurred in 2003 (7 horses) and 2006 (19 horses), but did not involve any research animals.

Behavior

Eight to ten bands were chosen from each of three populations for behavioral observations. These were selected from a stratified random sample consisting of bands with at least one stallion, one treated mare, and one control mare; however, natural interchange dictated that band compositions were plastic throughout the study. I observed the same bands at all 3 sites each year, unless mass interchange, mortalities,

removals, or other notable events made it unproductive to continue following the group. One band stallion died during the study and a new band was chosen to observe consisting of the same females previously observed with the original stallion.

Behavioral observations were separated into three daylight time periods: 0800–1200 hours, 1201–1600 hours, and 1601–2000 hours. I completed a minimum of nine observation sessions on each band in each time period, monthly from April to October, 2003–2006. Each observation session included collection of climatic (temperature, precipitation, cloud cover, wind speed), geographic (UTM and elevation), and temporal (time and date) data, a 20-minute instantaneous scan sample (Altmann 1974), at 1 minute intervals, of time budgets for each band member, all-occurrence data collection for social interactions (Altmann 1974), and spatial relationships between band members.

One-zero sampling (occurrence/non-occurrence of a specific behavior: Olson 1929, Altmann 1974) was less ideal than scan sampling for time budget data (Leger 1977) and continuous sampling for all behaviors was not considered a possibility due to the number of animals and observers involved. Mitlohner et al. (2001) found no significant difference between behavioral data recorded with scan sampling versus continuous sampling when intervals were 15 minutes or less, and found a high correlation between the techniques when using 1 minute intervals. In order to accurately record behaviors, I defined an ethogram which categorized specific behaviors into a suite of 15 discrete time budget categories (*see* Ransom and Cade 2009). These categories were agonism, comfort, elimination, feeding, grooming, harem social, harem tending, herding, interaction with humans, locomotion, out of sight, reproduction, resting, standing attentive, and submission.

Social interactions typically occur infrequently and last only a short duration of time, and therefore are difficult to quantify. Because instantaneous scan sampling has the potential to underestimate rare events (Houpt 1991, Doran 1992), I collected these specific social behavior data at every occurrence throughout each observation session. These all-occurrence behaviors included intraband social behaviors associated with herding, reproduction, agonistic and harem tending behaviors. Quantifying spatial relationships between band stallions and mares provided estimates of passive social interactions associated with the general behavior of the band (feeding, resting, or locomotion). This was done at the beginning of each observation session by estimating the distance (in horse-lengths) between each member of the observation band. Horse-length appeared to be a consistent metric for field use and was defined for analyses as 2.44 m based on the domestic horse industry standard.

I conducted all observations from distances that did not alert horses to the presence of the observer, and used 10 x 50 mm binoculars or a 16-45 x 60 mm spotting scope in situations where unaided observations were not adequate. A specific code was defined in the ethogram to denote when a horse's behavior indicated awareness of the observer and those data were omitted from analyses.

Most females were pregnant at the time of their first injection of PZP and some did not exhibit infertility after receiving treatment; therefore, to clarify behaviors associated with effective fertility control, all analyses considered animals to be in the treatment group only when they had been injected with 2 doses of PZP (primer and booster) and exhibited non-pregnancy. The few females that received PZP but continued

to produce young were omitted from analyses. Animals in the control group were not injected with PZP and exhibited pregnancy as it naturally occurred.

Covariates

I sought to identify factors that helped explain variation in horse behavior. To that end, I chose covariates for analyses that might reasonably be expected to influence behavior in equids. These included time of day, band fidelity, presence of dependent young, size of the band, body condition score, age, and experience of the polygynous male within a family group. The number of all horses present in the band at the time of the observation constituted the band size. Band composition data collected every 7 days, from April to October of each year, determined band fidelity: females were considered transient if they left their band and went to another band at least once during the season and resident if they never left during the season. Presence of young was recorded as a dependent foal from birth until to the end of that sampling season or documented death that season. Body condition of individuals was determined using a 10-step index similar to the Henneke et al. (1983) system; however, since these scores were determined solely by visual assessment (rather than palpation) in the field, the scale was adapted to a 0 to 5 score with half-step intervals as described by Rudman and Keiper (1991). This scale facilitated more consistent body condition score estimation in the field context. To compare these scales, a score of 3.5 on the Rudman and Keiper scale is roughly equivalent to 5 on the Henneke scale. Age was absolutely known for 88.4% of all individuals at Pryor Mountain, 42.1% of all individuals at Little Book Cliffs, and 34.2% of all individuals at McCullough Peaks from parturition records. An experienced veterinarian estimated ages for the remainder of animals in this study using dental

assessments during scheduled management captures. This method provides only approximate age due to the many external factors effecting tooth wear (Martin 2002). Tenure of males as polygynous band stallions in this study was unknown, so I assumed age was a reasonable indicator of band stallion experience. Age of the observed band stallions ranged 4–26 years, with mean age = 11.88 (95% CI: 10.43–13.33).

Analyses

The relative infrequency, and similar nature, of several time budget behaviors motivated me to aggregate them into broader categories for analysis. Grooming, comfort, standing attentive, and elimination were combined into maintenance; reproductive, harem tending, harem social, agonism, submission, and herding were combined into social; and interaction with humans and out of sight were combined into unknown. The time spent in the category of unknown ultimately did not differ between treatment groups in any population.

Most horses in this study were observed repeatedly over the course of 4 years; however, due to the nature of horses being difficult to find and/or unexpectedly moving out of view, the resulting samples were not equally distributed across individuals, nor were age cohorts equally represented. Repeated measures of individuals were accounted for by averaging data for each individual or pair of individuals per year. Observations were not averaged over the entire 4-year period because potentially important variables such as age, band fidelity, presence of a dependent foal, and treatment status often varied annually. Spatial relationship data were weighted by the number of hours the pairs of individuals were observed. Social interaction and time budget data were in count form and thus not weighted because they were analyzed as proportions.

I considered 26 hierarchical mixed effects candidate models, using the variables of treatment (*c*), band fidelity (*b*), foal presence (*f*), stallion age (*s*), body condition (*y*), and band size (*z*) as fixed effects, and the population (Little Book Cliffs, McCullough Peaks, and Pryor Mountain) as a random effect (Table 1). Social interaction data involved pairs of animals and the fixed effect of average distance between animals (*d*) was also considered for those analyses. Analyses of individual time budget behaviors and social interaction data were performed using the Hierarchical Linear Mixed Model function of SYSTAT 12[®] (SYSTAT Software, Inc. 2007) with estimates obtained by restricted maximum likelihood. The restricted maximum likelihood approach allowed for unbiased estimation of variance and freedom of assumption about a distribution (Patterson and Thompson 1971, Harville 1977).

Compositional analyses of time budget data were performed with a multi-response permutation procedure (MRPP) (Mielke and Berry 2007) using Blossom Statistical Software (Cade and Richards 2005). MRPP analyses used Monte Carlo resampling with 10,000 resamples to approximate the probabilities of a test statistic based on average Euclidean distances for detecting distributional differences. Spatial relationship analyses were conducted using the General Linear Model function in SYSTAT 12[®] because the mean distances between stallions and females were homogeneous across all three populations within each band behavior category (ANOVA: feeding: $F_{2,259}=1.38$, $P=0.253$; resting: $F_{2,233}=0.651$, $P=0.522$; locomotion: $F_{2,95}=0.617$, $P=0.542$).

I used minimum corrected Akaike's Information Criteria (AIC_c) to evaluate the strength of evidence for all linear and mixed models (Burnham and Anderson 2002).

Models achieving the greatest AIC_c weight were considered the best model for the predicted behavior, and all models exhibiting a ΔAIC_c of < 2 were considered plausible (Burnham and Anderson 2002). Compositional model selection was determined by summing the minimum AIC_c scores from each individually-modeled constituent behavior (feeding, resting, locomotion, maintenance, and social) and using the aggregate AIC_c score as strength of evidence for the overall composition (Ransom and Cade 2009). This procedure allowed detailed analyses of the individual behaviors without violation of the inherent compositional dependence.

Table 1. Candidate model set for analyses of feral horse behavior. For time budget and social interaction hierarchical linear mixed model analyses, i = random effect of the i th population (Little Book Cliffs, McCullough Peaks, and Pryor Mountain). For spatial relationship general linear model analyses, i is null. j = a vector of $1 \dots n$ observations for each population, where y =dependent variable and ϵ =statistical error. The intercept term, α_i , is inclusive of a fixed effect intercept + random effects intercepts. Categorical variable notation is inclusive of the unrepresented parameter value for each represented variable: b =band fidelity, c =treatment, f =foal presence, s =stallion age. The slope parameter for each continuous variable is noted as β_n , where d =mean distance between individuals, o =body condition, and z =band size.

Model	Model Specification	Model	Model Specification
1	$y_{ij} = \alpha_i + c_i + \epsilon_{ij}$	14	$y_{ij} = \alpha_i + c_i + b + \beta_2 d + f + \epsilon_{ij}$
2	$y_{ij} = \alpha_i + c_i + b + \epsilon_{ij}$	15	$y_{ij} = \alpha_i + c_i + b + f + (bf) + \epsilon_{ij}$
3	$y_{ij} = \alpha_i + c_i + f + \epsilon_{ij}$	16	$y_{ij} = \alpha_i + c_i + b + f + (cbf) + \epsilon_{ij}$
4	$y_{ij} = \alpha_i + c_i + \beta_1 o + \epsilon_{ij}$	17	$y_{ij} = \alpha_i + c_i + b + \beta_1 o + \beta_4 (cbo) + \epsilon_{ij}$
5	$y_{ij} = \alpha_i + c_i + \beta_2 d + \epsilon_{ij}$	18	$y_{ij} = \alpha_i + c_i + f + (cf) + \epsilon_{ij}$
6	$y_{ij} = \alpha_i + c_i + \beta_3 z + \epsilon_{ij}$	19	$y_{ij} = \alpha_i + c_i + \beta_1 o + \beta_5 (co) + \epsilon_{ij}$
7	$y_{ij} = \alpha_i + c_i + b + (cb) + \epsilon_{ij}$	20	$y_{ij} = \alpha_i + c_i + \beta_2 z + \beta_6 (cz) + \epsilon_{ij}$
8	$y_{ij} = \alpha_i + c_i + b + \beta_1 o + f + \beta_3 z + \epsilon_{ij}$	21	$y_{ij} = \alpha_i + c_i + \beta_2 d + \beta_7 (cd) + \epsilon_{ij}$
9	$y_{ij} = \alpha_i + c_i + b + \beta_1 o + \epsilon_{ij}$	22	$y_{ij} = \alpha_i + c_i + b + f + \epsilon_{ij}$
10	$y_{ij} = \alpha_i + c_i + b + \beta_1 o + f + \epsilon_{ij}$	23	$y_{ij} = \alpha_i + c_i + b + \beta_8 (bz) + \epsilon_{ij}$
11	$y_{ij} = \alpha_i + c_i + f + \beta_2 d + \epsilon_{ij}$	24	$y_{ij} = \alpha_i + c_i + \beta_8 (bz) + \epsilon_{ij}$
12	$y_{ij} = \alpha_i + c_i + b + f + \beta_2 d + \beta_3 z + \epsilon_{ij}$	25	$y_{ij} = \alpha_i + c_i + b + \beta_3 z + \epsilon_{ij}$
13	$y_{ij} = \alpha_i + c_i + b + \beta_2 d + \epsilon_{ij}$	26	$y_{ij} = \alpha_i + c_i + s + \epsilon_{ij}$

RESULTS

I conducted behavioral observations for 704 hours at Little Book Cliffs, 527 hours at McCullough Peaks, and 623 hours at Pryor Mountain, from 2003–2006. There was a strong correlation ($n=458$, $R^2=0.853$) between age of control females when conceiving and their rate of parturition the following year (Figure 1). This study focused on behaviors exhibited around the time of conception rather than the time of parturition and females were thus grouped for all behavior analyses into the following cohorts based on the different fecundity rates detected: 2–5 years, 6–14 years, and ≥ 15 years of age (ANOVA: $F_{3,454}=21.875$, $P<0.001$). No further analyses were conducted on the 1-year cohort because the sample size was small and highly unbalanced between treatment groups.

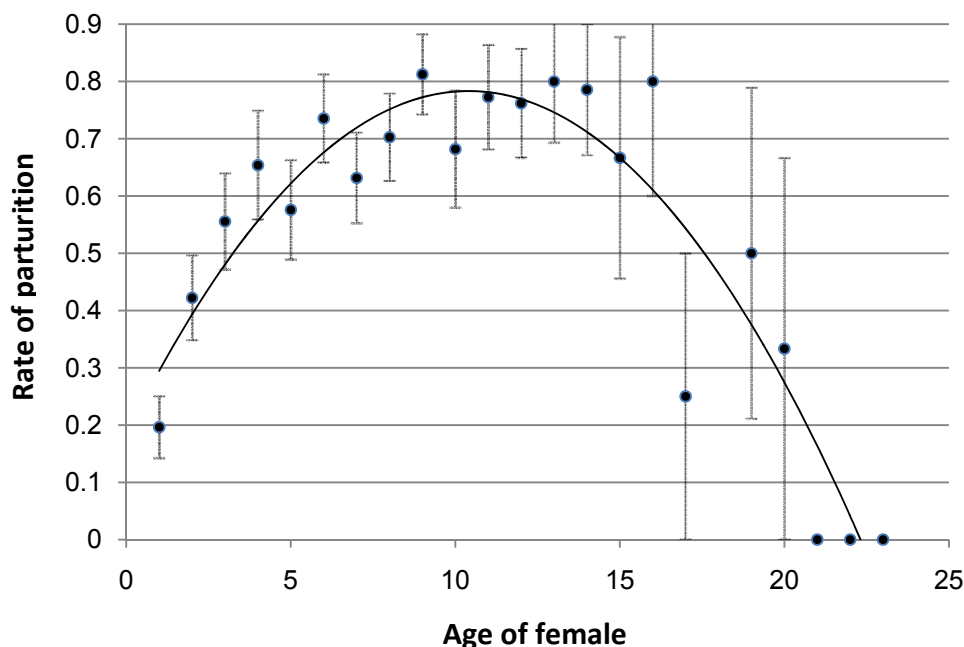


Figure 1. Rate of feral horse parturition as a function of control female age at the time of conception for the Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range populations, 2003–2006 ($n = 458$, $R^2 = 0.853$, $y = -0.006x^2 + 0.115x + 0.185$, vertical bars = standard error of the mean).

Climatic data of temperature, cloud cover, wind speed, and precipitation was very similar among locations and observations, although Pryor Mountain was slightly cooler and cloudier (Table 2). I did not further consider climate in behavior analyses due to this homogeneity of conditions. Likewise, behavioral observations were distributed equally across daylight time periods so I did not further consider time of day.

Table 2. Climate conditions during 2003–2006 behavioral observations at Little Book Cliffs Wild Horse Range (LBC), McCullough Peaks Herd Management Area (MCP), and Pryor Mountain Wild Horse Range (PRY). Each observation was 30 minutes in duration. Cloud cover, precipitation, and wind speed are given as percent of observations each climatic condition was present.

	Number of Observations	Temperature (mean °C ± SE)	Cloud Cover (Percent of observations)	Precipitation (Percent of observations)	Wind Speed (Percent of obs. < 16 kph)
LBC	1408	25.15 ± 1.32	42.25	4.88	88.51
MCP	1054	26.62 ± 1.80	45.43	3.78	91.25
PRY	1246	20.63 ± 1.17	51.40	5.25	88.00

Time Budgets

Compositional analyses revealed differences between treated and control females (6–14 years old) in allocation of time among feeding, resting, locomotion, maintenance and social behaviors (MRPP: $n=153$, $P<0.001$; figure 2). There was no difference detected between treatment groups in the less fecund groups of 2–5 year-olds (MRPP: $n=124$, $P=0.231$) and ≥ 15 year-olds (MRPP: $n=40$, $P=0.209$), although differences among other effects were supported in these cohorts. No single model showed support for all behaviors even though the dependent nature of the data dictates that a well-supported effect in one behavior must influence other behaviors in the composition (Ransom and Cade 2009). Feeding behavior for all age and treatment groups occupied the largest percentage of the daylight time budget, followed by resting behavior (figure 2).

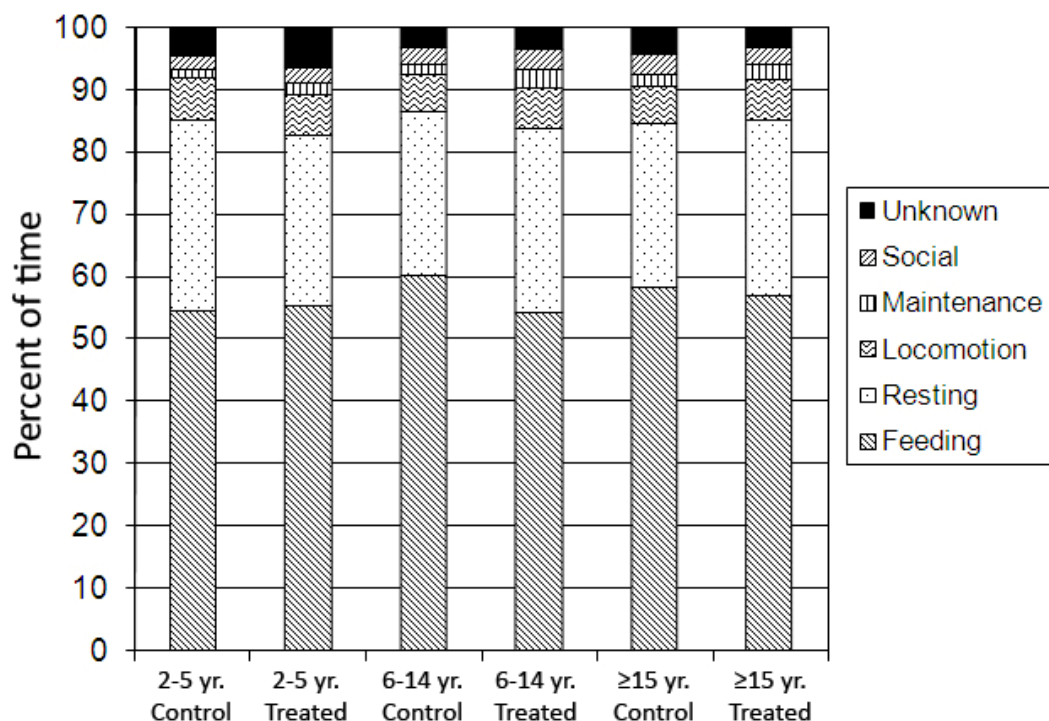


Figure 2. Hierarchical linear mixed model estimates (restricted maximum likelihood) for daylight time allocation of female feral horse behaviors in the 2- to 5-year-old (Model 1), 6- to 14-year-old (Model 4), and ≥ 15 year-old (Model 19) cohorts at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006. The models depicted were the most consistently supported for each behavior in the composition.

The most supported models for all behaviors in the 2- to 5-year cohort were Models 1 and 4, and body condition contributed significantly to feeding and social behaviors (table 3). Models 1 and 4 also were supported in the 6- to 14-year cohort (table 4), and both cohorts exhibited the same trend of increased feeding associated with lower body condition (2–5 yrs $\beta_1 = -0.110$; 6–14 yrs $\beta_1 = -0.109$); however, the trend was accompanied by considerable variation suggesting that other factors influence feeding time. Model 15 exhibited the most support for resting behavior (37.6% AIC_c weight) in 6- to 14-year-olds. This behavior was not well-supported by Models 1 and 4; likewise, Model 15 failed to explain all behaviors in the composition except resting. Model 15

estimated the interaction of band fidelity and foal presence to be a highly significant effect on resting behavior ($t_{133} = -3.546$, $P = 0.001$). Females with dependent foals rested less than females without foals (with foal $\bar{x} = 23.3\%$ time, 95% CI: 19.2–27.3%; without foal $\bar{x} = 31.4\%$ time, 95% CI: 27.2–35.6%). Transient mares with foals rested only 19.8% of the time (95% CI: 14.1–25.5%), whereas transient mares without foals rested 36.2% of the time (95% CI: 30.1–42.4%) (figure 3).

Table 3. Hierarchical linear mixed model estimates (restricted maximum likelihood) for the difference in means of compositional time budget behaviors for 2- to 5-year-old female feral horses ($n=124$) at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006. AIC_c weight represents the support received among all candidate models for each individual behavior. Composite AIC_c weight for Model 1=0.999, and Model 4=0.001 (Appendix B Table 2).

Model	Behavior	AIC_c weight	Effect	Difference	95% LCL	95% UCL	t	P
1	Feeding	0.288	Treatment	-0.009	-0.117	0.099	-0.157	0.875
	Resting	0.762	Treatment	0.035	-0.044	0.115	0.878	0.382
	Locomotion	0.881	Treatment	0.001	-0.048	0.051	0.057	0.955
	Maintenance	0.904	Treatment	-0.004	-0.023	0.015	-0.398	0.692
	Social	0.606	Treatment	-0.004	-0.030	0.022	-0.308	0.759
4	Feeding	0.485	Treatment	-0.001	-0.079	0.077	6.894	0.974
			Body Condition	-0.110	-0.194	-0.025	-2.569	0.011
	Resting	0.112	Treatment	0.031	-0.042	0.104	0.843	0.401
			Body Condition	0.039	-0.045	0.124	0.921	0.359
	Locomotion	0.025	Treatment	0.001	-0.048	0.051	0.051	0.959
			Body Condition	0.002	-0.020	0.024	0.147	0.883
	Maintenance	0.075	Treatment	-0.005	-0.024	0.014	-0.533	0.595
			Body Condition	0.012	-0.001	0.024	1.818	0.072
	Social	0.350	Treatment	-0.006	-0.028	0.017	-0.521	0.603
			Body Condition	0.020	0.005	0.035	2.673	0.009

Table 4. Hierarchical linear mixed model estimates (restricted maximum likelihood) for the difference in means of compositional time budget behaviors for 6- to 14-year-old female feral horses ($n=153$) at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006. AIC_c weight represents the support received among all candidate models for each individual behavior. Composite AIC_c weight for Model 1=0.534, and Model 4 =0.466 (Appendix B Table 2).

Model	Behavior	AIC_c weight	Effect	Difference	95% LCL	95% UCL	t	P
1	Feeding	0.366	Treatment	0.058	-0.028	0.144	1.341	0.182
	Resting	0.158	Treatment	-0.033	-0.094	0.029	-1.035	0.302
	Locomotion	0.709	Treatment	-0.004	-0.042	0.034	-0.194	0.846
	Maintenance	0.669	Treatment	-0.013	-0.043	0.016	-0.886	0.377
	Social	0.015	Treatment	-0.005	-0.039	0.028	-0.311	0.757
4	Feeding	0.333	Treatment	0.060	-0.017	0.137	1.548	0.124
			Body Condition	-0.109	-0.164	-0.054	-3.889	<0.001
	Resting	0.015	Treatment	-0.033	-0.092	0.027	-1.091	0.277
			Body Condition	0.022	-0.035	0.078	0.755	0.451
	Locomotion	0.262	Treatment	-0.005	-0.044	0.034	-0.243	0.809
			Body Condition	0.018	0.004	0.032	2.477	0.014
	Maintenance	0.302	Treatment	-0.014	-0.045	0.017	-0.902	0.368
			Body Condition	0.011	0.003	0.019	2.794	0.006
	Social	0.935	Treatment	-0.006	-0.038	0.025	-0.400	0.689
			Body Condition	0.026	0.014	0.038	4.167	<0.001

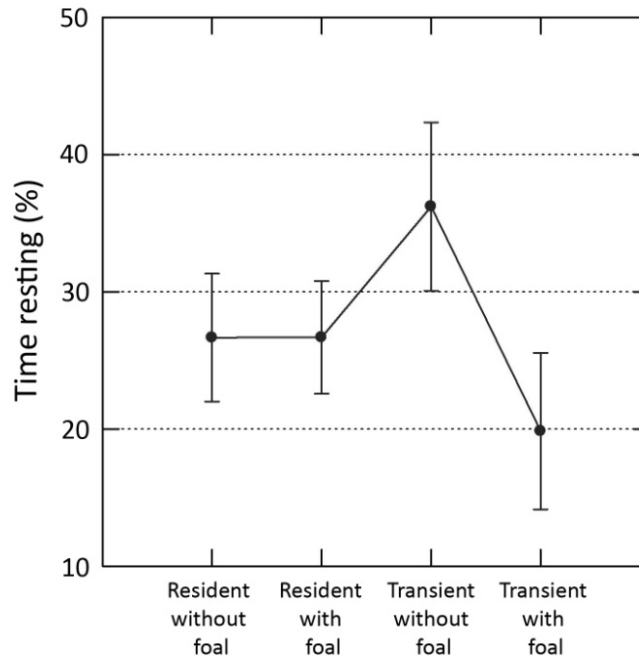


Figure 3. Least squares estimates (vertical bars=95% CI) of resting behavior rates for 6–14-year-old female feral horses ($n=142$) in hierarchical linear mixed model 15, differentiating between resident and transient females and those with and without a dependent foal. These data consist of horses from Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.

Supported models for ≥ 15 -year-olds exhibited a similar trade-off as the 6- to 14-year-olds, with Model 19 strongly supporting feeding and resting behaviors and Model 1 supporting all other behaviors (table 5). Model 19 estimated treated females fed less than control females (figure 4A), with body condition and interaction of treatment and body condition making strong contributions. The same model for resting behavior predicted treated females rested more than control females (figure 4B) and increasing resting behavior was associated with increasing body condition. It is important to note that while these differences are significant at higher and lower body condition scores, near the median score of 3.00 there is little difference between treatment groups.

Table 5. Hierarchical linear mixed model estimates (restricted maximum likelihood) for the difference in means of compositional time budget behaviors for ≥ 15 -year-old female feral horses ($n=40$) at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006. AIC_c weight represents the support received among all candidate models for each individual behavior. Composite AIC_c weight for Model 1=0.967, and Model 19=0.030 (Appendix B Table 2).

Model	Behavior	AIC_c weight	Effect	Difference	95% LCL	95% UCL	<i>t</i>	<i>P</i>
1	Feeding	0.043	Treatment	0.037	-0.045	0.120	0.920	0.364
	Resting	0.008	Treatment	-0.053	-0.154	0.047	-1.082	0.287
	Locomotion	0.447	Treatment	0.003	-0.048	0.055	0.125	0.901
	Maintenance	0.899	Treatment	-0.004	-0.029	0.021	-0.354	0.725
	Social	0.760	Treatment	0.003	-0.037	0.043	0.150	0.881
19	Feeding	0.826	Treatment	0.007	-0.065	0.080	-2.737	0.010
			Body Condition	-0.313	-0.482	-0.145	-3.785	0.001
			Treatment*Body Condition	0.290	0.079	0.500	2.802	0.009
	Resting	0.777	Treatment	-0.014	-0.087	0.059	2.328	0.026
			Body Condition	0.344	0.174	0.514	4.123	<0.001
			Treatment*Body Condition	-0.251	-0.464	-0.039	-2.409	0.022
	Locomotion	0.029	Treatment	-0.006	-0.058	0.046	-0.374	0.711
			Body Condition	-0.043	-0.092	0.007	-1.766	0.087
			Treatment*Body Condition	0.009	-0.051	0.070	0.315	0.754
	Maintenance	0.001	Treatment	-0.004	-0.029	0.021	-0.670	0.508
			Body Condition	-0.005	-0.031	0.021	-0.363	0.719
			Treatment*Body Condition	0.010	-0.022	0.042	0.608	0.547
	Social	0.016	Treatment	0.003	-0.044	0.050	1.926	0.063
			Body Condition	0.049	-0.006	0.104	1.800	0.081
			Treatment*Body Condition	-0.066	-0.134	0.003	-1.953	0.060

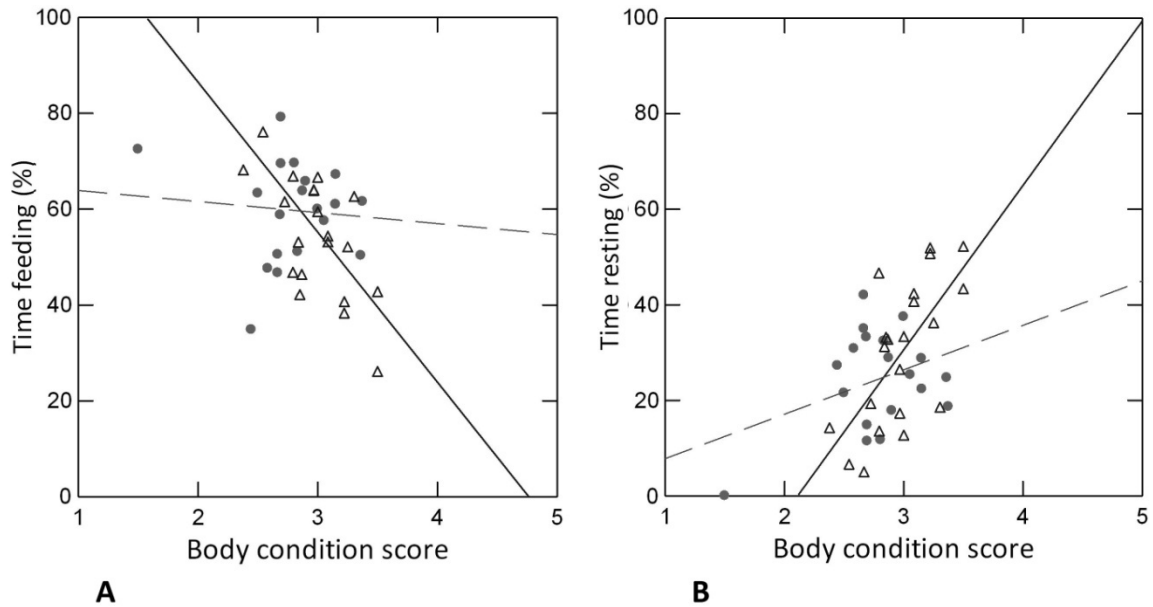


Figure 4. Hierarchical linear mixed model 19 for feeding (A) and resting (B) behavior in ≥ 15 -year-old control (●) and treated (△) female feral horses at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006 (dashed line= regression on control females, solid line= regression on treated females).

Social Interactions

Herding Behavior

Herding was the most commonly observed intraband social behavior at all 3 sites. Stallions were observed herding females at Little Book Cliffs at a mean rate of 0.20 (95% CI: 0.16–0.25) times per hour (tph), McCullough Peaks 0.17 (95% CI: 0.13–0.22) tph, and Pryor Mountain 0.68 (95% CI: 0.52–0.85) tph (figure 5). In the 2- to 5-year cohort, Model 2 for herding behavior exhibited most support in the data with 57.3% of the AIC_c weight, and Model 9, though very similar, followed with considerably less (table 6). Band fidelity contributed to the herding models for all age groups, and models containing this variable totaled 100% of the AIC_c weight for 2- to 5-year-olds, 99.3% for 6- to 14-

year-olds, and 98.0% for ≥ 15 -year-olds. There was no difference in the herding rate of 2- to 5-year-old females in Model 2.

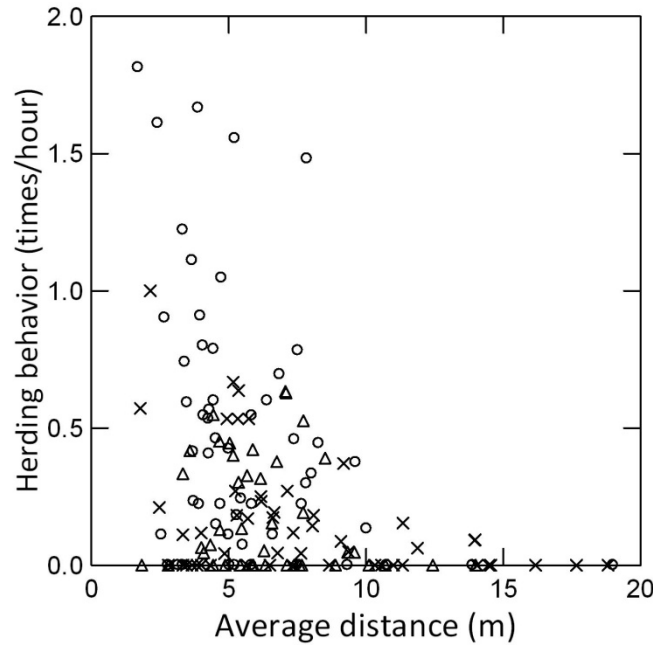


Figure 5. Herding behavior rate (times/hour) detected at Little Book Cliffs Wild Horse Range (Δ), McCullough Peaks Herd Management Area (X), and Pryor Mountain Wild Horse Range (\circ), 2003–2006, as a function of the average distance maintained between stallion-female pairs.

For 6- to 14-year-olds, Model 22 was the most supported candidate with 58.1% of the AIC_c weight, and control females were herded more in this cohort (figure 6). Foal presence contributed significantly to this model (table 6) and females without dependent foals were herded $\bar{x} = 0.37$ tph (95% CI: 0.19–0.56 tph) whereas females with dependent foals were herded $\bar{x} = 0.18$ tph (95% CI: 0.00–0.36 tph). Herding behavior in the ≥ 15 -year-old cohort was supported by Models 2 and 9 and there was no difference detected between treatment groups. Analyses of herding behavior toward females ≥ 15 -years-old was somewhat limited by the lack of animals in this cohort; consequently, the smaller sample size limited the candidate model set to Models 1–14 and 18–21 in order to avoid

over-parameterization. This limitation also held true for reproductive, harem tending, and agonistic behavior analyses.

Table 6. Hierarchical linear mixed model estimates (restricted maximum likelihood) of the difference in means, by female age cohort, for each fixed effect in the most supported models (all models with $\Delta AIC_c < 2$) of stallion-initiated social behavior at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.

Behavior	Female Cohort	Model	AIC_c weight	<i>N</i>	Effect	Difference	95% LCL	95% UCL	<i>t</i>	<i>P</i>
Herding	2–5 yr	2	0.573	92	Treatment	-0.333	-0.962	0.297	-1.050	0.297
					Band Fidelity	0.435	-0.198	1.067	1.367	0.175
	6–14 yr	22	0.581	128	Treatment	0.197	0.012	0.381	2.109	0.037
					Band Fidelity	0.203	-0.115	0.520	1.264	0.209
					Foal Presence	0.197	0.011	0.383	2.093	0.039
	≥15 yr	2	0.427	24	Treatment	-0.516	-1.190	0.158	-1.622	0.124
					Band Fidelity	-0.495	-1.390	0.400	-1.171	0.259
		9	0.359	24	Treatment	-0.420	-1.163	0.322	-1.200	0.248
					Band Fidelity	-0.422	-1.106	0.261	-1.309	0.209
					Body Condition	0.460	-0.326	1.246	1.240	0.233
Reproductive	2–5 yr	1	0.695	122	Treatment	-0.043	-0.117	0.030	2.724	0.247
	6–14 yr	1	0.523	151	Treatment	-0.078	-0.144	-0.013	-2.353	0.020
	≥15 yr	1	0.367	30	Treatment	0.076	-0.026	0.177	1.539	0.137
		26	0.150	30	Treatment	0.089	-0.006	0.184	1.934	0.065
					Stallion Age	0.015	0.004	0.027	2.734	0.012
Harem Tending	2–5 yr	5	0.594	122	Treatment	0.017	-0.060	0.093	0.427	0.670
					Distance	-0.001	-0.005	0.002	-0.662	0.509
	6–14 yr	4	0.752	151	Treatment	-0.055	-0.305	0.195	-0.436	0.664
					Body Condition	0.126	0.050	0.202	3.290	0.001
	≥15 yr	1	0.282	30	Treatment	-0.136	-0.344	0.073	-1.344	0.191
		4	0.249	30	Treatment	-0.132	-0.370	0.105	-1.152	0.261
Agonism	2–5 yr	1	0.885	122	Treatment	-0.005	-0.036	0.025	-0.333	0.739
	6–14 yr	1	0.711	151	Treatment	0.001	-0.029	0.031	0.059	0.953
	≥15 yr	1	0.866	30	Treatment	-0.010	-0.039	0.019	-0.716	0.481

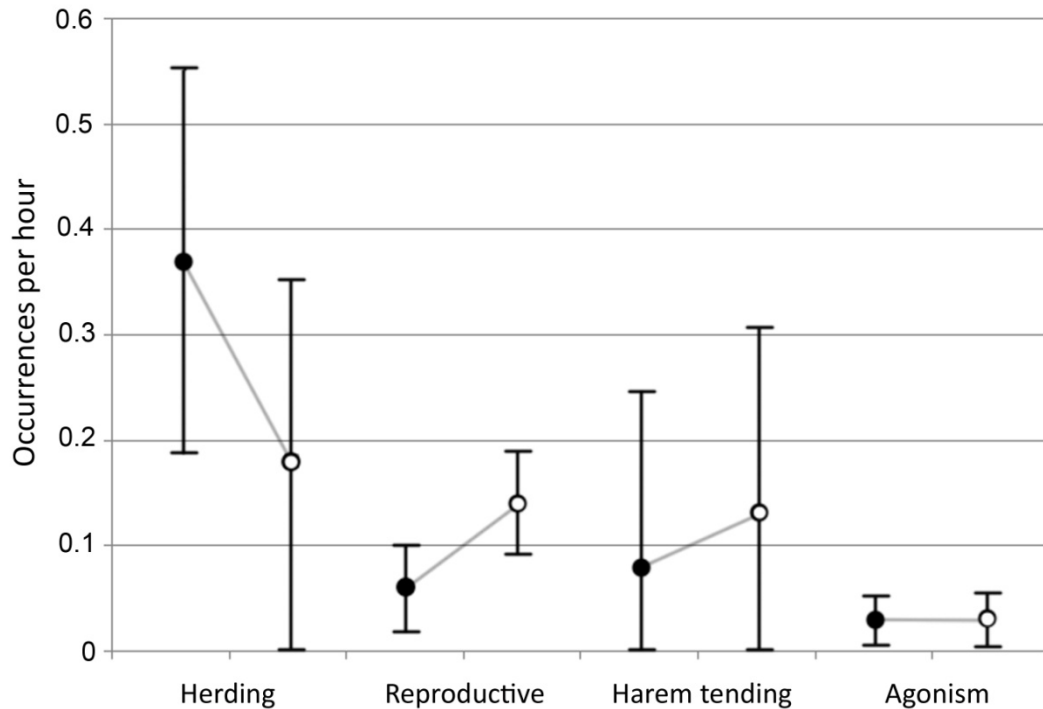


Figure 6. Hierarchical mixed model estimates (vertical bars = 95% CI) of herding (Model 22), reproductive (Model 1), harem tending (Model 4), and agonism (Model 1) behaviors for 6- to 14-year-old control (●) and treated (○) female feral horses at Little Book Cliffs Wild Horse Range, McCullough Peaks Herd Management Area, and Pryor Mountain Wild Horse Range, 2003–2006.

Reproductive Behavior

Reproductive behavior was the second most frequently observed intraband social behavior at all three sites. Little Book Cliffs stallions were observed exhibiting reproductive behavior toward females at a mean rate of 0.05 (95% CI: 0.02–0.09) tph, with McCullough Peaks stallions exhibiting the same rate of 0.05 (95% CI: 0.03–0.08) tph. Pryor Mountain stallions exhibited this behavior toward females at the rate of 0.10 (95% CI: 0.07–0.13) tph. The same model (Model 1) for all 3 age groups received the most support of AIC_c weight, but with varying percentages of weight within their group (table 6). Model 3 was the second most supported model in the 2- to 5-year-old and 6- to 14-year-old cohorts, and included foal presence as a fixed effect. The ≥ 15 -year group did

not have foal presence in the top 3 models, but the other plausible model of reproductive behavior in this cohort included a weak effect of treatment and a significant effect of stallion age.

Differences detected between treatment groups varied by female age. The most supported model for the 2- to 5-year-old cohort estimated mean reproductive interactions for control females at 0.03 (95% CI: 0.00–0.08) tph and treated females slightly higher at 0.08 (95% CI: 0.02–0.13) tph, which resulted in no statistical difference between treatment groups. However, there was a difference detected in the most fecund group of females, the 6- to 14-year-olds. Model 1 for this group estimated that treated females were the subject of stallion reproductive behaviors more than control females (figure 6). The ≥ 15 year-olds were estimated by Model 1 to have no difference in mean reproductive interactions (control $\bar{x} = 0.16$, 95% CI: 0.08–0.24 tph; treated $\bar{x} = 0.08$, 95% CI: 0.02–0.14), though Model 3 estimated a strong effect of stallion age, with the rate of reproductive behavior increasing proportionately with the increasing age of band stallions.

Harem Tending Behavior

Harem tending included occurrences of harem stallions defending females from other stallions as well as stealing females from other bands. Like herding and reproductive behaviors, this behavior was observed with greater frequency at Pryor Mountain, but was still relatively infrequent in all populations. Stallions exhibited harem tending behavior toward females at Pryor Mountain 0.17 (95% CI: 0.12–0.22) tph, whereas this was observed at Little Book Cliffs only 0.04 (95% CI: 0.03–0.05) tph and McCullough Peaks only 0.02 (95% CI: 0.01–0.03) tph. Model selection among harem

tending models disclosed a different lead candidate for each female cohort, and 2 models were plausible for the ≥ 15 -year-old cohort (table 6).

In the 2- to 5-year age group, the best model (Model 5) received 59.4% of the AIC_c weight and incorporated the covariate distance along with treatment. Distance did not contribute significantly to the overall model, but did assist in providing a marginally better fit with the data. This model estimated harem tending behavior toward 2- to 5-year-old control females ($\bar{x} = 0.05$, 95% CI: 0.00–0.10 tph) to be the same as treated females ($\bar{x} = 0.03$, 95% CI: 0.00–0.09). For 6- to 14-year-olds, treatment and body condition were included in the best model (Model 4), which received 75.2% of the AIC_c weight. In this model, stallions tended control and treated females equitably (figure 6). Body condition was a highly significant effect and females with higher body scores received more harem tending behaviors than lower body condition females. Models 1 and 4 were plausible candidates for harem tending in the ≥ 15 year-old cohort and neither estimated a significant difference between harem tending rates of the treatment groups. Model 4 indicated a weak effect of body condition on harem tending and like the 6- to 14-year-old cohort, females with higher body condition scores received more harem tending behaviors.

Agonistic Behavior

Agonistic behaviors from stallions toward female band members were observed 0.03 (95% CI: 0.01–0.05) tph at Little Book Cliffs, 0.01 (95% CI: 0.01–0.02) tph at McCullough Peaks, and 0.04 (95% CI: 0.03–0.06) tph at Pryor Mountain. In order of increasing intensity, 67.7% of these agonistic expressions were in the form of a threat, 1.7% were bumps or pushes, 26.8% were kicks or bites, and 3.8% were chases. Model 1

best explained the observed agonistic expressions in all 3 age classes with > 70% of the AIC_c weight (table 6). For 2- to 5- year-olds, stallions expressed similar amounts of agonism toward control and treated females (control $\bar{x}=0.03$ (95% CI: 0.00–0.05) tph, treated $\bar{x}=0.03$ (95% CI: 0.01–0.06) tph. Stallions also expressed agonism toward 6- to 14-year-old control and treated females at the same rates (figure 6). The ≥ 15 year-old cohort received fewer agonistic expressions from stallions, with control females receiving them 0.01 (95% CI: 0.00–0.03) tph and treated females receiving them 0.02 (95% CI: 0.00–0.04) tph.

Spatial Relationships

Spatial relationships between stallions and females were considered in three behavioral categories because the mean distances between horses differed significantly by the general behavior of the band (feeding, resting, or moving) (ANOVA: $F_{2,750}=59.820, P < 0.001$). Stallions maintained closest proximity to control females while bands were resting ($\bar{x} = 1.84$ m, 95% CI: 1.57–2.11 m) and slightly farther away while bands were in locomotion ($\bar{x} = 2.60$ m, 95% CI: 2.21–2.98 m). Bands were at their most dispersed structure when feeding ($\bar{x} = 3.44$ m, 95% CI: 2.83–4.05 m). Model 25 overwhelmingly provided the best fit in all 3 age cohorts while groups were feeding and no other candidate models were considered plausible (table 7). Band size contributed significantly to Model 25 in all 3 age groups, as did treatment for the 2- to 5-year-olds and band fidelity for 6- to 14-year-olds. Distance between horses in these models increased as band size increased. Stallions maintained closer proximity to 2- to 5-year-old treated females ($\bar{x} = 2.62$ m, 95% CI: 1.60–3.64 m) than to control females ($\bar{x} = 3.81$ m, 95% CI: 2.84–4.80 m). In the 6- to 14-year cohort, stallions maintained closer

distances to resident females (\bar{x} =2.96 m, 95% CI: 2.03–3.88 m) than to transient females (\bar{x} =4.03 m, 95% CI: 3.01–5.06 m).

Table 7. Analysis of Variance results for the difference in mean distance for each fixed effect in the most supported models of spatial relationships of male-female feral horse pairs at Little Book Cliffs, McCullough Peaks, and Pryor Mountain, 2003–2006, while bands were feeding. Significance is reported at the 95% level of confidence.

Female Cohort	Model	AIC _c weight	<i>n</i>	Effect	<i>F</i>	<i>P</i>
2 to 5 years old	25	0.983	107	Treatment	14.173	<0.001
				Band Fidelity	0.539	0.459
				Band size	13.375	<0.001
6 to 14 years old	25	0.764	132	Treatment	0.708	0.397
				Band Fidelity	11.004	0.001
				Band size	11.602	0.001
≥15 years old	25	0.996	25	Treatment	0.466	0.476
				Band Fidelity	0.675	0.511
				Band size	17.042	<0.001

When bands were in a resting state, Models 24, 7, 2, and 25 were plausible candidates for spatial relationships between stallions and 2- to 5-year-old females (table 8). Band fidelity was included in all of these models and the most supported model by AIC_c weight included the interaction of treatment and band fidelity. Resident females in all four models exhibited similar spatial relationships with stallions as transient females. Model 25 for 6- to 14-year-old females and Model 23 for ≥15-year-old females estimated band fidelity as a significant effect while the bands were resting. Resident females in the 6- to 14-year-old group (\bar{x} =1.78 m, 95% CI: 1.22–2.34 m) stayed closer to stallions than transient females (\bar{x} =2.32 m, 95% CI: 1.67–2.97 m), as did females in the ≥15-year-old cohort (resident \bar{x} =1.86 m, 95% CI: 1.07–2.64 m; transient \bar{x} =1.58 m, 95% CI: 0.00–3.44 m). In both 6- to 14-year-old and ≥15-year-old groups, the influence of band size

was significant, and as band size increased, so did the distance between stallions and band females.

Table 8. Analysis of Variance results for the difference in mean distance for each fixed effect in the most supported models of spatial relationships of male-female feral horse pairs at Little Book Cliffs, McCullough Peaks, and Pryor Mountain, 2003–2006, while bands were resting. Significance is reported at the 95% level of confidence.

Female Cohort	Model	AIC _c weight	<i>n</i>	Effect	<i>F</i>	<i>P</i>
2 to 5 years old	24	0.290	92	Treatment	1.905	0.171
				Band Fidelity x Band Size	2.533	0.115
	7	0.225	92	Treatment	3.111	0.081
				Band Fidelity	2.384	0.126
				Treatment x Band Fidelity	2.323	0.131
	2	0.208	92	Treatment	1.966	0.164
				Band Fidelity	1.877	0.174
	25	0.169	92	Treatment	2.585	0.112
				Band Fidelity	2.271	0.135
				Band size	1.762	0.188
6 to 14 years old	25	0.656	124	Treatment	1.503	0.223
				Band Fidelity	4.296	0.040
				Band size	6.062	0.015
≥15 years old	23	0.529	25	Treatment	0.608	0.445
				Band Fidelity	8.937	0.008
				Band Fidelity x Band Size	20.497	<0.001
	25	0.437	25	Treatment	0.114	0.739
				Band Fidelity	0.255	0.619
				Band size	19.844	<0.001

Spatial relationships during locomotion in the 2- to 5-year-old cohort were explained by Models 24, 23, 25, and 2, with Model 24 attaining 42.2% of the AIC_c weight (table 9). There was no difference in estimated distance between stallions and control females (\bar{x} = 2.46 m, 95% CI: 1.71–3.21 m) and stallions and treated females (\bar{x} = 2.24 m, 95% CI: 1.22–3.26 m) in this age group, although the interaction of band

fidelity and band size was significant. Resident control females maintained closer proximity to stallions than transient females.

In the 6- to 14-year-old age group, Model 7 for locomotion was the most supported candidate and estimated no difference in spatial relationships between stallions and control females (\bar{x} = 2.80 m, 95% CI: 1.74–3.85 m) versus treated females (\bar{x} = 3.96 m, 95% CI: 2.48–5.44 m). Band fidelity was an important variable in this model and both band fidelity and the interaction of treatment and band fidelity contributed significantly. The most notable difference detected was the closer proximity of stallions to resident control females (\bar{x} = 2.87 m, 95% CI: 1.86–3.88 m) versus transient treated females (\bar{x} = 5.98 m, 95% CI: 3.64–8.32 m). Spatial relationships for the ≥ 15 -year-old cohort in locomotion could not be analyzed because the small sample size paired with some missing covariate data resulted in complete loss of degrees of freedom in most candidate models. The null model estimated no difference between treatment groups in this cohort ($F_{1,10}=0.105$, $P=0.753$).

Table 9. Analysis of Variance results for the difference in mean distance for each fixed effect in the most supported models of spatial relationships of male-female feral horse pairs at Little Book Cliffs, McCullough Peaks, and Pryor Mountain, 2003–2006, while bands were in locomotion. Significance is reported at the 95% level of confidence.

Female Cohort	Model	AIC _c weight	<i>n</i>	Effect	<i>F</i>	<i>P</i>
2 to 5 years old	24	0.422	39	Treatment	0.127	0.723
				Band Fidelity x Band Size	7.302	0.010
	23	0.209	39	Treatment	0.060	0.808
				Band Fidelity	1.130	0.295
				Band Fidelity x Band Size	3.016	0.091
	25	0.162	39	Treatment	0.394	0.534
				Band Fidelity	6.083	0.019
				Band Size	2.521	0.121
	2	0.156	39	Treatment	0.216	0.645
				Band Fidelity	5.154	0.029
6 to 14 years old	7	0.514	50	Treatment	1.673	0.202
				Band Fidelity	4.640	0.037
				Treatment x Band Fidelity	5.365	0.025

DISCUSSION

Estimates of time budget allocations for all age and treatment groups fell within the broad ranges previously reported for equids (Mayes and Duncan 1986, Boyd et al. 1988, Berger et al. 1999). While the compositional analyses of time budget detected a statistically significant difference in how 6- to 14-year old treated and control females allocated their time, the analyses of individual behaviors in the composition did not attribute this disparity to contraceptive treatment in any single behavior. Differences were detected in the effects of body condition, band fidelity, and foal presence between treatment groups in this age cohort. There was moderate to strong support for differences in feeding and resting behavior related to contraceptive treatment group in the ≥ 15 -year-olds. All of these results are somewhat contrary to Powell's (1999, 2000) finding of no

difference in time allocation between PZP-treated and control horses and Rogers' (2001) conclusion that the younger treated cohort spent more time feeding. These differences are not surprising because both previous studies only focused on a single population for a short time period and my study illustrated that differences in some behavioral expressions between populations may exist (see figure 6). There is some caution in interpreting Powell's results because the females used as controls in his study had all been previously treated with PZP and were only considered uncontracepted because they were not currently vaccinated. Kirkpatrick et al. (1992) reported that latency effects of immunocontraception with PZP vary both from one individual to another, and by years of successive treatment prior to cessation of treatment. It is therefore unknown if the control mares in Powell's study were biologically fertile.

Rogers (2001) found that PZP had no effect on time spent walking, grooming, or standing in feral horses, and likewise, Heilmann et al. (1998) found no differences in time spent moving or idling between PZP-treated and untreated free-ranging female elk. My results are synonymous with these studies, and it appears that the complex social organization of feral horses does not greatly influence the time allocation of these basic maintenance behaviors. McShea et al. (1997) did note that PZP-treated female white-tailed deer (*Odocoileus virginianus*) spent more time running or walking than untreated females, but social structure and reproductive strategy of white-tailed deer is distinctly different from that of elk and horses.

The difference in time budget behaviors between treatment groups appears somewhat minimal on first inspection, but the more detailed analyses depict significant differences among covariate effects between treatment groups. Foal presence, band

fidelity, and body condition were important effects in how horses managed their time. Van Dierendonck et al. (2004) reported that mares without foals spent less time resting and a greater percent of time in social interaction than either pregnant or post-partum mares. The most supported model of resting behavior in my study exhibited strong support for the effect of foal presence in the 6- to 14-year-olds, but with contrary results. Mares with dependent foals rested less than their barren counterparts, and the effect was even more pronounced when interacting with band fidelity. This differing result may be attributed to the social structure (absence of stallions) in van Dierendonck et al.'s (2004) study, compared to the free-roaming natural populations that experienced threats of predation and competition among stallions in my study. Females with dependent young simply had to be more vigilant when faced with these natural constraints on their time.

The significantly small amount of time spent resting by transient mares with foals is an important consideration when evaluating the effects of fertility control in horses since it concerns potential physiological changes that may have implications toward long-term health and lifetime fitness. Assuming that PZP applications are reasonably effective might lead to the conclusion that this combination of factors should be relatively rare in a population; however, 16.9% of the 6- to 14-year-olds ($n=142$) in my study fit these criteria. The treated animals in this group resulted from the lag-time in contraceptive effect that occurs from females typically being treated when they are already pregnant, leading to a subsequent year of infertility while caring for a dependent foal. Linklater et al. (1999) found transient mares had poorer body condition than resident mares as a result of greater harassment by stallions, and Nuñez et al. (2009) found that immunocontracepted female feral horses in an island population exhibited a decrease in

band fidelity during the non-breeding season. Further investigation into the effects of fertility control on band fidelity should be conducted to determine the scope and extent of this relationship in immunocontracepted female horses during the breeding season.

Body condition contributed to individual time budget behaviors in all age classes, with lower body condition females feeding more than higher condition females. The body condition scores of females in my study were relatively homogeneous and investigation into this phenomenon may require a wider range of conditions to illicit more in depth results. The trend detected, however, does signify that more detailed analyses of body condition between treatment groups are warranted since many proximate mechanisms driving body condition were not investigated. Social dominance in relation to body condition has been attributed to food gain and energy expenditure (Hogstad 1987, Cuthill and Houston 1997) and stochastic climate events could cause depressed or elevated states of body condition and lead to greater differences between treatment groups. Fischhoff et al. (2007) also found that resource needs related to lactation in female zebras (*Equus burchellii*) were associated with intraband dominance. Turner and Kirkpatrick (horses: 2002) and McShea et al. (white-tailed deer: 1997) found that contracepted females exhibit higher body condition than control females, and Conner et al. (elk: 2007) found a seasonal difference in winter body condition of females, but no overall difference between fertility control treatment groups. Boyd (horses: 1988) found pregnant females spent more time feeding than barren females, and the National Research Council (1978) attributed higher body condition of barren females to the high energetic costs of pregnancy and lactation. This interpretation suggests that treated females may be allocating time differently due primarily to a change in nutritional needs.

The finer-scale analyses of social behavior disclosed that 6- to -14-year-old treated females exhibited more reproductive behaviors than control animals in the same cohort. This was expected given the higher rates of estrous reported in PZP-treated females compared to control females (Mahi-Brown 1985, Shumake and Wilhelm 1995, Heilmann et al. 1998, Curtis et al. 2002). Heilmann et al. (1998) found that PZP-treated female elk exhibited higher rates of sexual interaction outside of the breeding season than did untreated females. Powell (1999, 2000) also found that increased reproductive tending and mating duration of stallions lasted longer as a result of mares continuing their estrous cycles into the fall, which he proposed may contribute to a disruption in band stability. Similarly, McShea et al. (1997) found changes in the extended breeding season behavior of white-tailed deer males, in addition to an earlier start of breeding behavior in the subsequent year after females were treated. My study did not examine the seasonality of reproductive behavior, though additional research should determine the scope of this potential effect as it may have implications toward stallion body condition and consequent lifetime fitness. The effect of more frequent reproductive behavior in treated females in my study may be counteracted by increased herding behavior of control females in the same cohort, making the energetic difference between treatment groups appear negligible.

Herding behavior relates to the high energetic cost of locomotion for both the male and female(s) involved. Rogers (2001) found that the percentage of time females were herded by males was different between treatment groups and significant effects of presence/absence of a foal and band fidelity were detected. Even when generalized across 3 populations, I also detected that presence/absence of a dependent foal

contributed strongly to herding behavior and that control females were herded more often. The primary implication from this finding is that the presence or absence of foals may influence herding behavior, which is a fundamental mechanism of maintaining integrity of the social group. Ultimately this relates to band fidelity: the greater herding rate of control females, paired with the closer mean distance between stallions and resident females, suggests that treated females may be more likely to become transient and thus incur the changes detected in time budget allocations.

Harem tending and agonistic behaviors by stallions did not differ among treatment groups, but stallions invested more harem tending behaviors in mares with higher body condition in the most fecund group. This result was not robust, however, and body condition scores were insufficiently heterogeneous to test if this phenomenon would persist across the full range possible scores. Optimality theory may explain this finding by the perceived fitness pay-off the stallion would receive from investing in animals more likely to contribute offspring (McArthur and Pianka 1966), but the true nature of this somewhat weak relationship has not been explained by my analyses.

No difference in frequency of agonistic behaviors was expressed by stallions toward control and treated females, but this is not surprising since most agonistic expressions within feral horse bands are expressed between females in order to establish and facilitate dominance (Houpt et al. 1978, Waring 1983, Keiper and Receveur 1992, Weeks et al. 2000). Stallions are generally not the most dominant member of the band and this is thought to result from the greater time spent away from the group while defending or recruiting females (Keiper and Receveur 1992). While little has been investigated regarding agonism and contraception in feral horses, some data has been

published in regard to agonism as related to presence of a foal and band fidelity. Estep et al. (1993) found no change in agonistic behaviors associated with presence or absence of a dependent foal, and Rutberg and Greenberg (1990) found frequency of aggression did not vary between females of transient and resident status. My study concurs with these results as the covariates of interest were not present in the most supported models of agonistic behavior, and were not significant effects in the candidate models that contained them.

Spatial relationships within bands represent the passive social interaction between band members. The role of equids in free-roaming populations that experience natural predation and competition implies that spatial distance maintained by the stallion to members of his band is directly related to investment in those individuals. Van Dierendonck et al. (2004) found that females formed groups based on reproductive status. This could imply a systemic difference in spatial relationships between a stallion and females in different fertility control treatment groups. Estep et al. (1993) also found that females were spatially less affiliated with other females after parturition, leading to a greater space-management challenge for stallions. Perhaps the most problematic factor in determining the influence of fertility control on spatial relationships is the reported pair-bonding, or preference of some individuals to remain near each other based on no clear biological explanation (Klimov 1988, Pickeral et al. 1993). My results show a difference in mean distance between stallions and mares based on behavior of the band, but no support was found for differences between treatment groups in the most fecund or oldest cohorts. The 2- to 5-year-olds exhibited a highly significant treatment effect in spatial relationships while bands were feeding. Heitor et al. (2006) found that lower ranking

females formed stronger bonds with stallions, but the stallions also preferred less genetically-related females for spatial proximity. This may provide partial explanation for the 2- to 5-year-old spatial relationship results, but there is no clear functional explanation based on my study. The expected differences based on Estep et al. (1993) and van Dierendonck et al. (2004) were not detected, but this may be explained by the inherently female focus and lack of predation pressure in their studies. The Powell (1999, 2000) study was conducted in a free-roaming population and did not detect any spatial differences between stallions and treated/control group females. Powell's study was not age-structured, and Rogers (2001) did not investigate spatial relationships, so no further comparisons are possible. Band size made a strong contribution to the most supported models of spatial relationships in my study, which is not surprising given that larger band sizes fundamentally necessitate larger distances between individuals. This result does support the ability of the candidate models to capture some basic functional properties of the biological system and illustrates that variance in social organization may influence behavioral differences between populations.

CONCLUSION

Immunocontraception with PZP provided an exceptional opportunity to investigate behavior of ungulates with complex social systems. However, this treatment also presented challenges in separating the influence of confounding variables. My study detected minimal direct effects of PZP treatment on the behavior of feral horses. The rate of reproductive behavior in the most fecund age cohort was the only acute effect attributed to the sole variable of treatment, which was an expected result. Though

statistical support was found for some differences in time budget behaviors, the immediate biological significance between treatment groups appeared to be minimal.

Differences that were detected between treatment groups were associated mostly with secondary effects that may be products of fertility control, such as presence of a dependent foal, change in body condition, and resident or transient nature of females in band. It is largely unknown how the relationships of band fidelity and foal presence relate to the underlying behavioral ecology of feral horses, though they may have influence on long-term band structure and social networks, changes to dominance hierarchies, pair-bonding, and socialization. These topics have broader implications than the results presented in this study and imply more dynamic changes to the ecology of feral horses. Body condition of stallions may also warrant consideration for additional study because the energetically counteractive effects of some social behaviors directed toward females in each treatment group are not obtained by the stallions initiating those effects.

The results from this study depict differences in behaviors between populations, which is likely a response to habitat-use by bands in the population. Most social behaviors estimated by this study found higher rates of occurrence at Pryor Mountain than the other two sites; consequently, Pryor Mountain also exhibits a focused habitat-use profile resulting in close proximity of bands to each other. McCullough Peaks and Little Book Cliffs experience a more widely distributed habitat-use profile and lower social interaction rates between bands. This proximity of groups to one another introduces different levels of social pressure between bands and illustrates that some populations may be more sensitive to fertility control management strategies than others.

Considerations of vaccination timing and number of females treated in the population may influence the magnitude of any behavioral changes observed. The results from my study partially mitigate these anomalous effects by using the mixed effect model approach over multiple years, but managers should assess their population to determine how these results may apply to the ecological structure they are managing.

The results presented here offer statistical analyses based only on the candidate model set and support is given for the best models in that set. This does not preclude the possibility that some important variables were not evaluated, but the support found for expected effects portrays the ability of the models to capture at least some biological basis for the behaviors evaluated. Behavioral analyses rarely capture effects attributed to individual temperament of animals, which may have influenced the results reported here. I feel confident that the large sample sizes and my multiple population approach addressed this issue to the extent possible and exposed important foundations for explaining the influences of immunocontraception on animal behavior.

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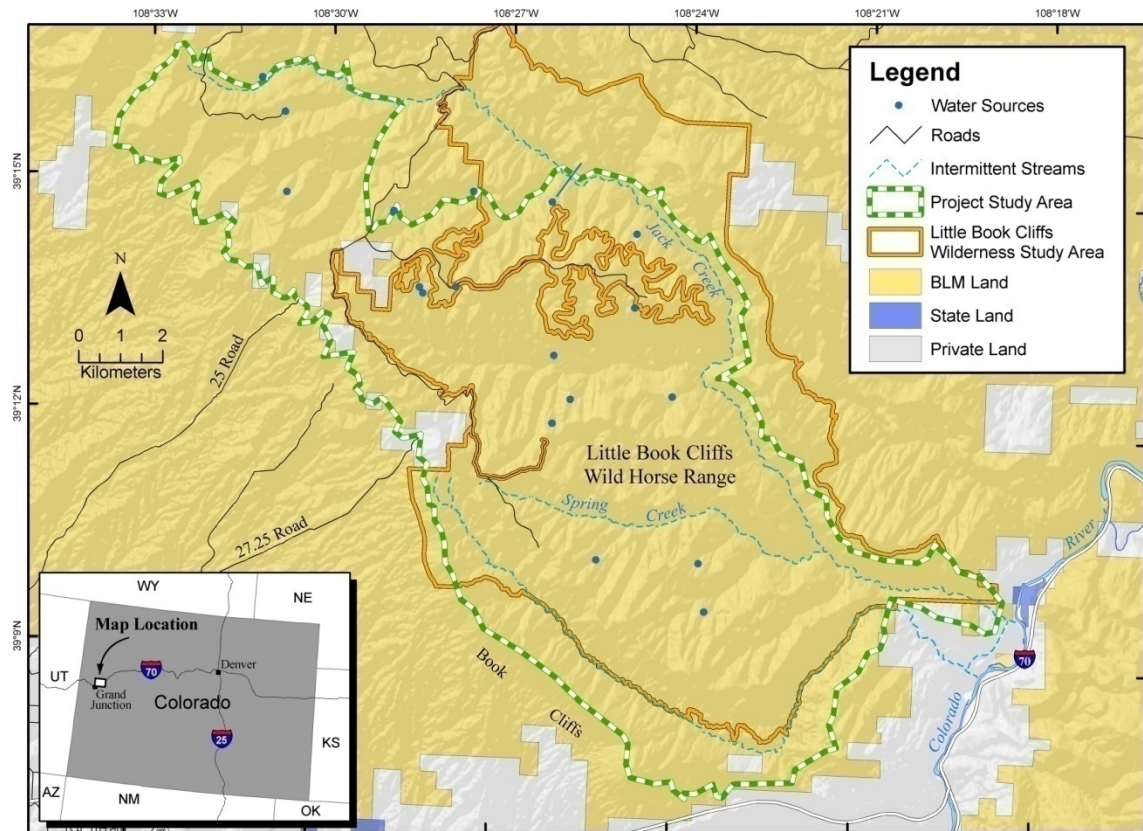
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APPENDIX A

Study area locations and population structures



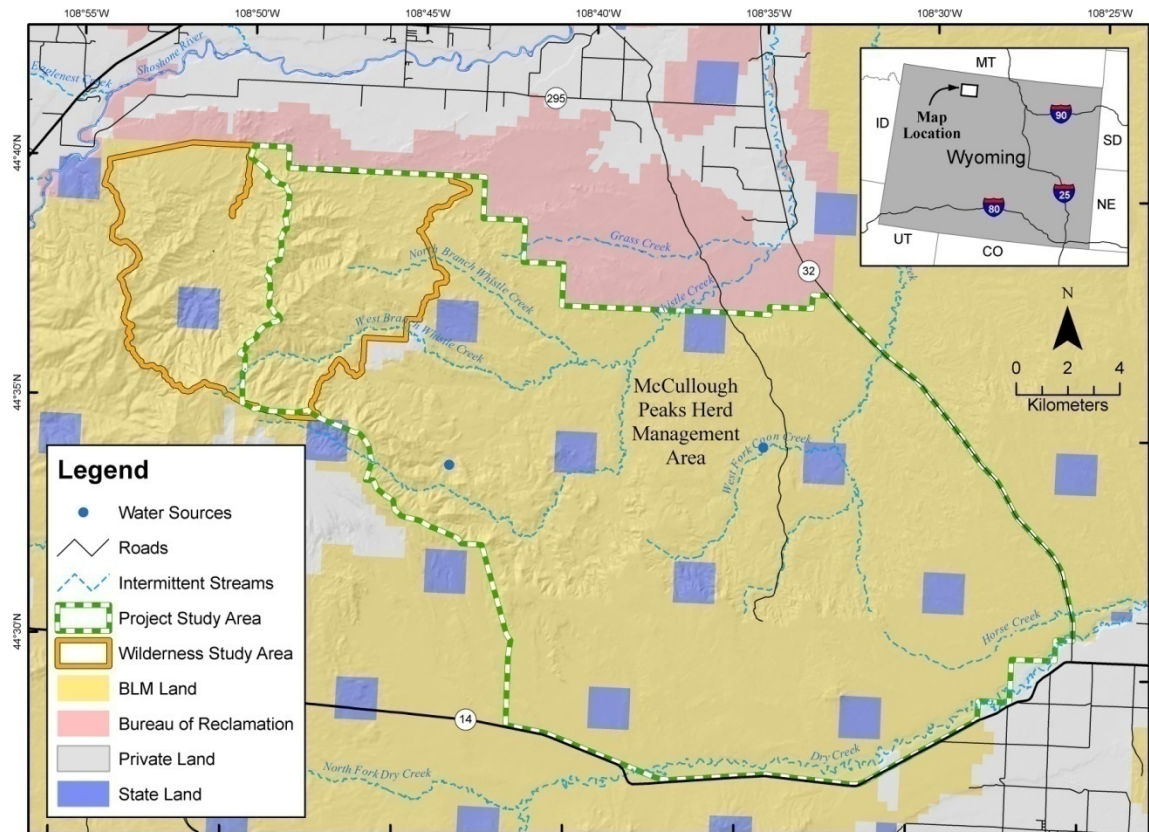
Appendix A Figure 1. Location of the Little Book Cliffs Wild Horse Range and study area boundaries.

Appendix A Table 1. Little Book Cliffs Wild Horse Range feral horse population composition from 2003–2006, as calculated on September 30 of each year.

Cohort	2003	2004a	2004b*	2005	2006
Adult Male	59	59	42	44	49
Adult Untreated Female [†]	34	41	33	41	49
Adult Treated Female	24	24	24	23	22
Adult Unknown	0	0	0	0	0
Foal Male	13	11	1	6	9
Foal Female	22	7	3	7	7
Foal Unknown	2	5	5	0	3
Yearling Male	7	15	4	2	6
Yearling Female	8	22	8	6	7
Yearling Unknown	0	1	0	1	0
Missing	10	19	19	19	18
Adult Mortalities	2	3	1	1	1
Yearling Mortalities	0	0	0	0	0
Foal Mortalities	2	0	1	2	3
Management removal	0	0	68	0	0
Total Herd	169–179	185–204	120–139	130–149	152–170

* 2004b was calculated on October 31, 2004 after a management removal of horses from the range.

[†] Adult females not currently treated, including control and formerly-treated individuals.



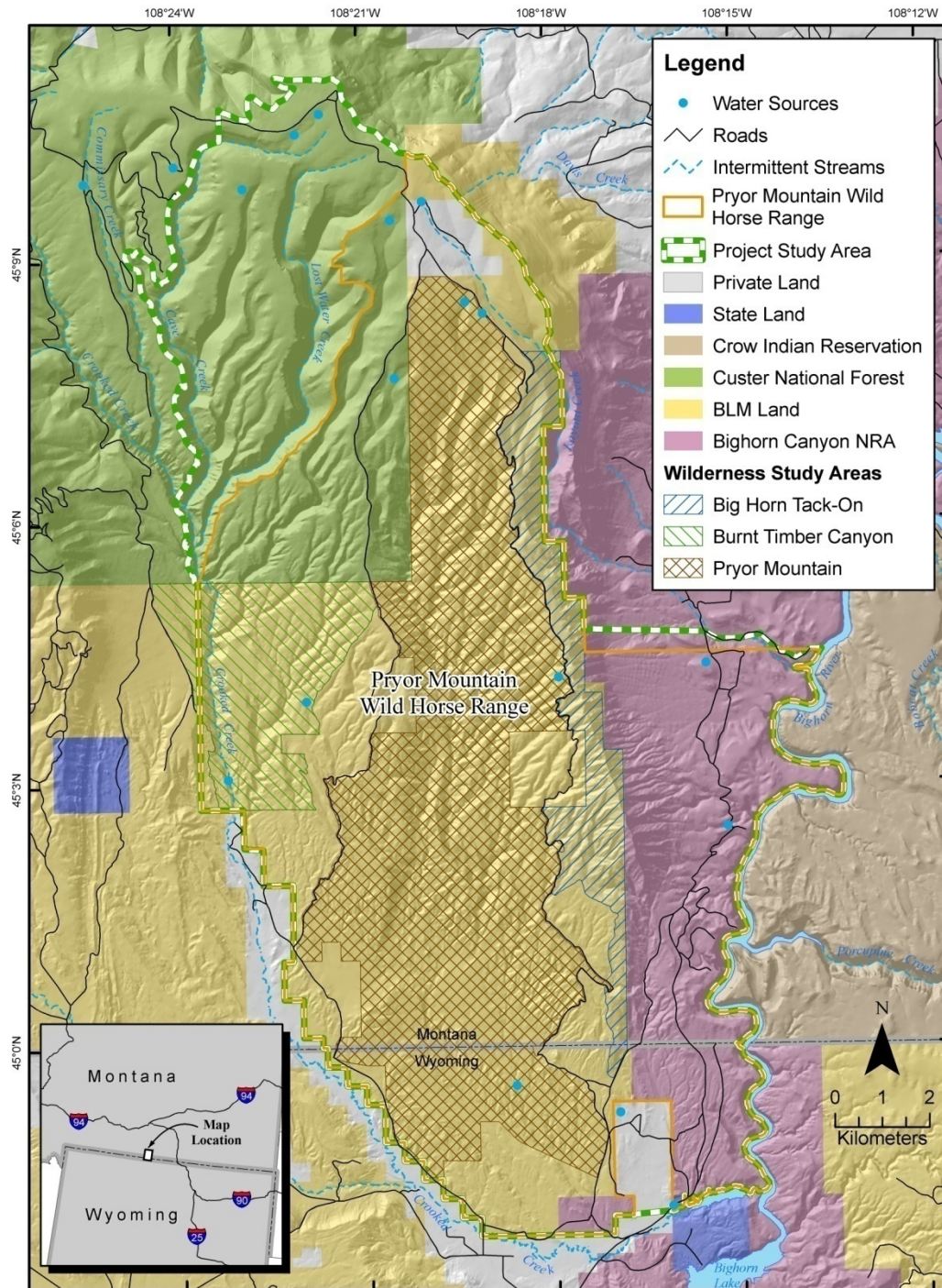
Appendix A Figure 2. Location of the McCullough Peaks Herd Management Area and study area boundaries.

Appendix A Table 2. McCullough Peaks Herd Management Area feral horse population composition from 2003–2006, as calculated on September 30 of each year.

Cohort	2003	2004	2004b*	2005	2006
Adult Male	126	159	62	47	45
Adult Untreated Female [†]	115	143	4	10	12
Adult Treated Female	0	0	36	36	36
Adult Unknown	31	11	0	0	0
Foal Male	31	39	5	17	7
Foal Female	16	17	2	17	9
Foal Unknown	34	42	0	0	0
Yearling Male	30	39	0	8	16
Yearling Female	15	20	3	2	16
Yearling Unknown	12	23	0	0	0
Missing	2	2	3	12	11
Adult Mortalities	3	0	1	0	1
Yearling Mortalities	0	0	1	0	0
Foal Mortalities	1	2	0	0	1
Management removal	0	0	379	0	0
Total Herd	410–412	493–495	112–115	137–152	141–152

* 2004b was calculated on October 31, 2004 after a management removal of horses from the range.

[†] Adult females not currently treated, including control and formerly-treated individuals.



Appendix A Figure 3. Location of the Pryor Mountain Wild Horse Range and study area boundaries.

Appendix A Table 3. Pryor Mountain Wild Horse Range feral horse population composition during 2003-2006, as calculated on September 30 of each year.

Cohort	2003	2004	2005	2006
Adult Male	66	69	71	52
Adult Untreated Female [†]	44	54	48	45
Adult Treated Female	18	8	19	21
Adult Unknown	0	0	0	0
Foal Male	12	2	13	16
Foal Female	10	2	14	13
Foal Unknown	0	0	1	0
Yearling Male	8	2	1	7
Yearling Female	4	5	0	6
Yearling Unknown	0	0	0	0
Missing	6	12	1	6
Adult Mortalities	5	1	0	2
Yearling Mortalities	0	15	0	2
Foal Mortalities	8	24	8	6
Management removal	7	0	0	19
Total Herd	162–168	142–154	167–168	150–156

[†] Adult females not currently treated, including control and formerly-treated individuals.

APPENDIX B

Model Selection

Appendix B Table 1. The four best fit models in each age cohort for individual daylight time budget behaviors: FE=feeding rate (observations/hour), RE=resting rate, LO=locomotion rate, MT=maintenance rate, SO=social rate, i=th population (Little Book Cliffs, McCullough Peaks, Pryor Mountain), j=a vector of observations for each population, y=dependent variable, and ϵ =statistical error. The intercept term, α_i , is inclusive of a fixed effect intercept + random effects intercepts. Categorical variable notation is inclusive of the unrepresented parameter value for each represented variable: b=band fidelity, c=treatment, f=foal presence, s=stallion age. The slope parameter for each continuous variable is noted as β_d , where d=mean distance between individuals, o=body condition, and z=band size. Models are ranked by lowest AIC_c score, and consequent highest AIC_c weight (Burnham and Anderson 2002). Models exhibiting a Δ AIC_c of < 2 were considered plausible.

Cohort	Model	Model Specification	N	AIC _c	Δ AIC _c	Likelihood	AIC _c weight
2 to 5 years old	4	$FE_{ij} = \alpha_i + c_i + \beta_1 O + \epsilon_{ij}$	124	-116.78	0.00	1.000	0.485
	1	$FE_{ij} = \alpha_i + c_i + \epsilon_{ij}$	124	-115.73	1.05	0.592	0.288
	19	$FE_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \epsilon_{ij}$	124	-114.95	1.83	0.400	0.194
	3	$FE_{ij} = \alpha_i + c_i + f + \epsilon_{ij}$	124	-110.43	6.36	0.042	0.020
6 to 14 years old	1	$FE_{ij} = \alpha_i + c_i + \epsilon_{ij}$	153	-144.56	0.00	1.000	0.366
	4	$FE_{ij} = \alpha_i + c_i + \beta_1 O + \epsilon_{ij}$	153	-144.37	0.19	0.911	0.333
	19	$FE_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \epsilon_{ij}$	153	-143.33	1.23	0.541	0.198
	3	$FE_{ij} = \alpha_i + c_i + f + \epsilon_{ij}$	153	-141.41	3.15	0.207	0.076
≥15 years old	19	$FE_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \epsilon_{ij}$	40	-46.19	0.00	1.000	0.814
	4	$FE_{ij} = \alpha_i + c_i + \beta_1 O + \epsilon_{ij}$	40	-41.61	4.58	0.102	0.083
	1	$FE_{ij} = \alpha_i + c_i + \epsilon_{ij}$	40	-40.29	5.89	0.053	0.043
	18	$FE_{ij} = \alpha_i + c_i + f + (cf) + \epsilon_{ij}$	40	-38.45	7.74	0.021	0.017
2 to 5 years old	1	$RE_{ij} = \alpha_i + c_i + \epsilon_{ij}$	124	-118.43	0.00	1.000	0.726
	4	$RE_{ij} = \alpha_i + c_i + \beta_1 O + \epsilon_{ij}$	124	-114.70	3.73	0.155	0.112
	3	$RE_{ij} = \alpha_i + c_i + f + \epsilon_{ij}$	124	-113.62	4.82	0.090	0.065
	19	$RE_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \epsilon_{ij}$	124	-113.25	5.18	0.075	0.054
6 to 14 years old	15	$RE_{ij} = \alpha_i + c_i + b + f + (bf) + \epsilon_{ij}$	142	-165.42	0.00	1.000	0.376
	7	$RE_{ij} = \alpha_i + c_i + b + (cb) + \epsilon_{ij}$	142	-165.16	0.26	0.877	0.330
	1	$RE_{ij} = \alpha_i + c_i + \epsilon_{ij}$	153	-163.69	1.73	0.420	0.158
	3	$RE_{ij} = \alpha_i + c_i + f + \epsilon_{ij}$	153	-161.09	4.33	0.115	0.043
≥15 years old	19	$RE_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \epsilon_{ij}$	40	-45.55	0.00	1.000	0.777
	4	$RE_{ij} = \alpha_i + c_i + \beta_1 O + \epsilon_{ij}$	40	-42.73	2.82	0.244	0.189
	9	$RE_{ij} = \alpha_i + c_i + b + \beta_1 O + \epsilon_{ij}$	39	-37.12	8.44	0.015	0.011
	1	$RE_{ij} = \alpha_i + c_i + \epsilon_{ij}$	40	-36.44	9.12	0.010	0.008
2 to 5 years old	1	$LO_{ij} = \alpha_i + c_i + \epsilon_{ij}$	124	-452.90	0.00	1.000	0.881
	6	$LO_{ij} = \alpha_i + c_i + \beta_3 Z + \epsilon_{ij}$	124	-446.85	6.05	0.049	0.043
	3	$LO_{ij} = \alpha_i + c_i + f + \epsilon_{ij}$	124	-446.85	6.05	0.049	0.043
	4	$LO_{ij} = \alpha_i + c_i + \beta_1 O + \epsilon_{ij}$	124	-445.76	7.14	0.028	0.025

Appendix B Table 1 continued on the next page

Appendix B Table 1 continued

Cohort	Model	Model Specification	N	AIC _c	ΔAIC _c	Likelihood	AIC _c weight
6 to 14 years old	1	$LO_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	153	-575.51	0.00	1.000	0.709
	4	$LO_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	153	-573.51	1.99	0.369	0.262
	19	$LO_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \varepsilon_{ij}$	153	-567.50	8.00	0.018	0.013
	3	$LO_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	153	-567.33	8.17	0.017	0.012
≥15 years old	1	$LO_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	40	-136.82	0.00	1.000	0.447
	4	$LO_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	40	-136.48	0.34	0.844	0.377
	3	$LO_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	40	-134.30	2.52	0.284	0.127
	19	$LO_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \varepsilon_{ij}$	40	-131.36	5.46	0.065	0.029
2 to 5 years old	1	$MT_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	124	-584.84	0.00	1.000	0.904
	4	$MT_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	124	-579.86	4.97	0.083	0.075
	3	$MT_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	124	-576.41	8.43	0.015	0.013
	19	$MT_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \varepsilon_{ij}$	124	-574.33	10.51	0.005	0.005
6 to 14 years old	1	$MT_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	153	-751.10	0.00	1.000	0.670
	4	$MT_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	153	-749.51	1.59	0.452	0.302
	19	$MT_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \varepsilon_{ij}$	153	-743.29	7.81	0.020	0.013
	3	$MT_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	153	-742.81	8.29	0.016	0.011
≥15 years old	1	$MT_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	40	-192.21	0.00	1.000	0.899
	3	$MT_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	40	-187.04	5.17	0.075	0.068
	4	$MT_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	40	-184.26	7.95	0.019	0.017
	6	$MT_{ij} = \alpha_i + c_i + \beta_3 Z + \varepsilon_{ij}$	40	-183.49	8.72	0.013	0.011
2 to 5 years old	1	$SO_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	124	-542.86	0.00	1.000	0.606
	4	$SO_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	124	-541.76	1.10	0.578	0.350
	19	$SO_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \varepsilon_{ij}$	124	-536.91	5.96	0.051	0.031
	3	$SO_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	124	-534.05	8.81	0.012	0.007
6 to 14 years old	4	$SO_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	153	-617.35	0.00	1.000	0.935
	19	$SO_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \varepsilon_{ij}$	153	-611.47	5.89	0.053	0.049
	1	$SO_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	153	-609.14	8.21	0.016	0.015
	3	$SO_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	153	-600.80	16.56	0.000	0.000
≥15 years old	1	$SO_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	40	-131.92	0.00	1.000	0.760
	6	$SO_{ij} = \alpha_i + c_i + \beta_3 Z + \varepsilon_{ij}$	40	-127.80	4.12	0.128	0.097
	3	$SO_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	40	-127.21	4.71	0.095	0.072
	4	$SO_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	40	-125.68	6.25	0.044	0.033

Appendix B Table 2. Compositional model selection for each age group using aggregated AIC_c scores ($aAIC_c$). $aAIC_c$ scores are the sums AIC_c scores from the individual time budget behavior models (feeding+resting+ locomotion+maintenance+social behaviors for each candidate model). Models are ranked by lowest $aAIC_c$ score, and consequent highest $aAIC_c$ weight.

Cohort	Model	$aAIC_c$	$\Delta aAIC_c$	Likelihood	$aAIC_c$ weight
2 to 5 years old	1	-1814.76	0	1	0.999
	4	-1798.87	15.90	0.000	0.001
	19	-1782.16	32.60	0.000	0.000
6 to 14 years old	1	-2243.99	0	1	0.534
	4	-2243.71	0.27	0.872	0.466
	19	-2222.94	21.05	0.000	0.000
≥ 15 years old	1	-537.682	0	1	0.967
	19	-530.758	6.92	0.031	0.030
	4	-525.457	12.23	0.002	0.002

Appendix B Table 3. The four best fit models in each age group for stallion behavior directed toward females, where AG = agonism rate (observations/hour), HD = herding rate, HT = harem tending rate, RP = Reproductive behavior rate, i = i th population (Little Book Cliffs, McCullough Peaks, Pryor Mountain), j =a vector of observations for each population, y =dependent variable, and ϵ =statistical error. The intercept term, α_i , is inclusive of a fixed effect intercept + random effects intercepts. Categorical variable notation is inclusive of the unrepresented parameter value for each represented variable: b=band fidelity, c=treatment, f=foal presence, s=stallion age. The slope parameter for each continuous variable is noted as β_n , where d=mean distance between individuals, o=body condition, and z=band size. Models are ranked by lowest AIC_c score, and consequent highest AIC_c weight (Burnham and Anderson 2002). Models exhibiting a ΔAIC_c of < 2 were considered plausible.

Cohort	Model	Model Specification	N	AIC_c	ΔAIC_c	Likelihood	AIC_c weight
2 to 5 years old	2	$HD_{ij} = \alpha_i + c_i + b + \epsilon_{ij}$	92	209.16	0.00	1.000	0.572
	9	$HD_{ij} = \alpha_i + c_i + b + \beta_1 o + \epsilon_{ij}$	92	211.17	2.01	0.366	0.210
	13	$HD_{ij} = \alpha_i + c_i + b + \beta_2 d + \epsilon_{ij}$	92	213.19	4.19	0.123	0.070
	10	$HD_{ij} = \alpha_i + c_i + b + \beta_1 o + f + \epsilon_{ij}$	92	213.35	4.03	0.134	0.076
6 to 14 years old	22	$HD_{ij} = \alpha_i + c_i + b_i + f_i + \epsilon_i$	128	151.90	0.00	1.000	0.581
	9	$HD_{ij} = \alpha_i + c_i + b + \beta_1 o + \epsilon_{ij}$	128	154.26	2.36	0.307	0.178
	10	$HD_{ij} = \alpha_i + c_i + b + \beta_1 o + f + \epsilon_{ij}$	128	154.75	2.85	0.240	0.140
	12	$HD_{ij} = \alpha_i + c_i + b + f + \beta_2 d + \beta_3 z + \epsilon_{ij}$	128	157.36	5.47	0.065	0.038
≥ 15 years old	2	$HD_{ij} = \alpha_i + c_i + b + \epsilon_{ij}$	24	46.23	0.00	1.000	0.427
	9	$HD_{ij} = \alpha_i + c_i + b + \beta_1 o + \epsilon_{ij}$	24	46.57	0.35	0.842	0.359
	10	$HD_{ij} = \alpha_i + c_i + b + \beta_1 o + f + \epsilon_{ij}$	24	50.13	3.90	0.142	0.061
	13	$HD_{ij} = \alpha_i + c_i + b + \beta_2 d + \epsilon_{ij}$	24	50.16	3.94	0.140	0.060

Appendix B Table 3 continued on the next page

Appendix B Table 3 continued

Cohort	Model	Model Specification	N	AIC _c	ΔAIC _c	Likelihood	AIC _c weight
2 to 5 years old	1	$RP_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	122	-99.83	0.00	1.000	0.695
	3	$RP_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	122	-97.30	2.53	0.282	0.196
	4	$RP_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	122	-94.61	5.22	0.074	0.051
	18	$RP_{ij} = \alpha_i + c_i + f + (cf) + \varepsilon_{ij}$	122	-93.80	6.03	0.049	0.034
6 to 14 years old	1	$RP_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	151	-76.86	0.00	1.000	0.523
	3	$RP_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	151	-74.79	2.06	0.356	0.186
	4	$RP_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	151	-74.20	2.65	0.266	0.139
	18	$RP_{ij} = \alpha_i + c_i + f + (cf) + \varepsilon_{ij}$	151	-72.98	3.88	0.144	0.075
≥15 years old	1	$RP_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	30	-26.39	0.00	1.000	0.367
	26	$RP_{ij} = \alpha_i + c_i + s + \varepsilon_{ij}$	30	-24.61	1.78	0.410	0.150
	6	$RP_{ij} = \alpha_i + c_i + \beta_3 Z + \varepsilon_{ij}$	30	-23.33	3.07	0.216	0.079
	2	$RP_{ij} = \alpha_i + c_i + b + \varepsilon_{ij}$	24	-23.28	3.11	0.211	0.078
2 to 5 years old	5	$HT_{ij} = \alpha_i + c_i + \beta_2 d + \varepsilon_{ij}$	122	-268.84	0.00	1.000	0.594
	1	$HT_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	122	-266.18	2.66	0.265	0.157
	4	$HT_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	122	-265.81	3.03	0.220	0.131
	11	$HT_{ij} = \alpha_i + c_i + f + \beta_2 d + \varepsilon_{ij}$	122	-264.45	4.39	0.111	0.066
6 to 14 years old	4	$HT_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	151	-92.64	0.00	1.000	0.752
	19	$HT_{ij} = \alpha_i + c_i + \beta_1 O + \beta_5 (CO) + \varepsilon_{ij}$	151	-88.35	4.29	0.117	0.088
	1	$HT_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	151	-88.34	4.30	0.117	0.088
	3	$HT_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	151	-86.77	5.87	0.053	0.040
≥15 years old	1	$HT_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	30	1.55	0.00	1.000	0.282
	4	$HT_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	30	1.81	0.25	0.881	0.249
	3	$HT_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	30	4.00	2.45	0.294	0.083
	2	$HT_{ij} = \alpha_i + c_i + b + \varepsilon_{ij}$	24	7.60	6.04	0.049	0.020
2 to 5 years old	1	$AG_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	122	-296.48	0.00	1.000	0.884
	6	$AG_{ij} = \alpha_i + c_i + \beta_3 Z + \varepsilon_{ij}$	122	-290.55	5.93	0.052	0.046
	3	$AG_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	122	-289.75	6.73	0.035	0.031
	4	$AG_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	122	-289.57	6.91	0.032	0.028
6 to 14 years old	1	$AG_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	151	-283.51	0.00	1.000	0.711
	3	$AG_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	151	-281.12	2.39	0.303	0.215
	18	$AG_{ij} = \alpha_i + c_i + f + (cf) + \varepsilon_{ij}$	151	-277.13	6.38	0.041	0.029
	4	$AG_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	151	-276.67	6.84	0.033	0.023
≥15 years old	1	$AG_{ij} = \alpha_i + c_i + \varepsilon_{ij}$	30	-97.10	0.00	1.000	0.866
	3	$AG_{ij} = \alpha_i + c_i + f + \varepsilon_{ij}$	30	-91.08	6.02	0.049	0.043
	18	$AG_{ij} = \alpha_i + c_i + f + (cf) + \varepsilon_{ij}$	30	-91.08	6.02	0.049	0.043
	4	$AG_{ij} = \alpha_i + c_i + \beta_1 O + \varepsilon_{ij}$	30	-90.03	7.07	0.029	0.025

Appendix B Table 4. The 4 best fit models in each age group for stallion spatial relationship (mean annual distance) to females while bands were in feeding (SF), resting (RE), and in locomotion (LO); α =intercept, ϵ =statistical error, b =band fidelity, c =treatment, d =mean distance between individuals, f =foal presence, s =stallion age, o =body condition, and z =band size. The slope parameter for each continuous variable is noted as β_n , where d =mean distance between individuals, o =body condition, and z =band size. Models are ranked by lowest AIC_c score, and consequent highest AIC_c weight (Burnham and Anderson 2002). Models exhibiting a ΔAIC_c of < 2 were considered plausible.

Female Cohort	Model	Model Specification	N	AIC_c	ΔAIC_c	Likelihood	AIC_c weight
2 to 5 years old	22	$SF = \alpha + c + b + \beta_3 z + \epsilon$	107	847.40	0.00	1.000	0.983
	23	$SF = \alpha + c + b + \beta_8(bz) + \epsilon$	107	857.61	10.21	0.006	0.006
	7	$SF = \alpha + c + b + (cb) + \epsilon$	107	858.40	11.00	0.004	0.004
	2	$SF = \alpha + c + b + \epsilon$	107	858.71	11.31	0.004	0.003
6 to 14 years old	22	$SF = \alpha + c + b + \beta_3 z + \epsilon$	132	1091.79	0.00	1.000	0.764
	23	$SF = \alpha + c + b + \beta_8(bz) + \epsilon$	132	1095.54	3.75	0.153	0.117
	24	$SF = \alpha + c + \beta_8(bz) + \epsilon$	132	1095.72	3.94	0.140	0.107
	2	$SF = \alpha + c + b + \epsilon$	132	1100.95	9.16	0.010	0.008
≥ 15 years old	22	$SF = \alpha + c + b + \beta_3 z + \epsilon$	25	205.88	0.00	1.000	0.996
	24	$SF = \alpha + c + \beta_8(bz) + \epsilon$	25	218.59	12.71	0.002	0.002
	2	$SF = \alpha + c + b + \epsilon$	25	219.09	13.21	0.001	0.001
	7	$SF = \alpha + c + b + (cb) + \epsilon$	25	220.19	14.32	0.001	0.001
2 to 5 years old	24	$SR = \alpha + c + \beta_8(bz) + \epsilon$	92	394.20	0.00	1.000	0.290
	7	$SR = \alpha + c + b + (cb) + \epsilon$	92	394.70	0.51	0.776	0.225
	2	$SR = \alpha + c + b + \epsilon$	92	394.86	0.66	0.718	0.208
	25	$SR = \alpha + c + b + \beta_3 z + \epsilon$	92	395.28	1.08	0.583	0.169
6 to 14 years old	25	$SR = \alpha + c + b + \beta_3 z + \epsilon$	124	611.65	0.00	1.000	0.656
	23	$SR = \alpha + c + b + \beta_8(bz) + \epsilon$	124	614.12	2.47	0.290	0.190
	2	$SR = \alpha + c + b + \epsilon$	124	615.58	3.93	0.140	0.092
	7	$SR = \alpha + c + b + (cb) + \epsilon$	124	617.51	5.86	0.053	0.035
≥ 15 years old	23	$SR = \alpha + c + b + \beta_8(bz) + \epsilon$	25	97.10	0.00	1.000	0.529
	25	$SR = \alpha + c + b + \beta_3 z + \epsilon$	25	97.49	0.38	0.826	0.437
	24	$SR = \alpha + c + \beta_8(bz) + \epsilon$	25	102.66	5.56	0.062	0.033
	2	$SR = \alpha + c + b + \epsilon$	25	110.63	13.52	0.001	0.001
2 to 5 years old	24	$SL = \alpha + c + \beta_8(bz) + \epsilon$	39	161.52	0.00	1.000	0.422
	23	$SL = \alpha + c + b + \beta_8(bz) + \epsilon$	39	162.92	1.40	0.496	0.209
	25	$SL = \alpha + c + b + \beta_3 z + \epsilon$	39	163.43	1.91	0.384	0.162
	2	$SL = \alpha + c + b + \epsilon$	39	163.50	1.98	0.371	0.156
6 to 14 years old	7	$SL = \alpha + c + b + (cb) + \epsilon$	50	240.94	0.00	1.000	0.514
	24	$SL = \alpha + c + \beta_8(bz) + \epsilon$	50	243.47	2.53	0.283	0.145
	25	$SL = \alpha + c + b + \beta_2 z + \epsilon$	50	243.48	2.54	0.281	0.145
	2	$SL = \alpha + c + b + \epsilon$	50	243.98	3.04	0.219	0.112

BEHAVIOR GLOSSARY

Agonism: Aggressive behavior between two individuals, including: threats, bumping, pushing, biting, kicking, chasing, rearing, striking, boxing, and dancing

Comfort: Self-enjoyment expression, including: play, investigation, sun-basking, shelter seeking, and masturbation

Elimination: Urination or defecation not associated with harem social, harem tending, or reproductive behavior

Feeding: Ingestion of nutrients by grazing, browsing, eating snow, drinking, mineral licking, coprophagy, and pawing at food resources

Grooming: Self-grooming behavior associated with pelage health and insect control, including: rolling, shaking, nibbling, licking, tail-swishing, rubbing, and stomping to displace insects

Harem social: Social interaction between band members that is not specifically indicative of reproduction, harem tending, or agonism, including: allogrooming, olfactory investigation (as expressed in pair-bonding), and vocal communication

Harem tending: Stallion behaviors that are directed at maintaining the harem, including: defense of females, systematic marking of female eliminations, depositing feces on a midden, and recruitment of females from another band

Herding: Stallion behavior directed at driving females in his harem together or in a specific direction, typically expressed as snaking with his head held low and sweeping side-to-side while in pursuit of the female(s)

Interaction with humans: Focal animal became aware of observer or other human in the area and is focused on them

Locomotion: Moving from one location to another, including: walking, trotting, cantering, galloping, jumping, and swimming

Maintenance: Aggregate of comfort, elimination, grooming, and standing attentive behaviors

Out of sight: Focal animal disappeared from view due to rapid locomotion or dense vegetation

Reproduction: Sexual interaction between two individuals, including: reproductive tending by a stallion (flehmen, vocalization, flank rubbing, and penis drop), solicitation by a female (estrous, presentation, vocalization), successful and unsuccessful copulation, forced copulation, mare rejection and mare acceptance.

Resting: Relaxed, inattentive state in a standing or recumbent position

Social: Aggregate of agonism, harem tending, harem social, herding, reproduction, and submission behaviors

Standing attentive: Alert, focused response to a real or perceived stimulus, typically expressed with rigid body posture and ears and eyes directed at the stimulus (*see* Interaction with humans for exception)

Submission: Behavior exhibited in retreat from an agonist, typically expressed with lowered head, lowering of hindquarters, laid down ears, and/or jaw snapping

Unknown: Aggregate of interaction-with-humans and out-of-sight categories