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Quantifying Equid Behavior—A Research Ethogram for Free-Roaming Feral Horses

Techniques and Methods 2-A9

U.S. Department of the Interior
U.S. Geological Survey

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Contents

Figures

Quantifying Equid Behavior—A Research Ethogram for Free-Roaming Feral Horses

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Introduction

Feral horses (*Equus caballus*) are globally distributed in free-roaming populations on all continents except Antarctica and occupy a wide range of habitats including forest, grassland, desert, and montane environments. The largest populations occur in Australia and North America and have been the subject of scientific study for decades, yet guidelines and ethograms for feral horse behavioral research are largely absent in the scientific literature. The U.S. Geological Survey (USGS) Fort Collins Science Center conducted research on the influences of the immunocontraceptive porcine zona pellucida (PZP) on feral horse behavior from 2003–2006 in three discrete populations in the American west (see Ransom and others, 2007; Ransom, 2009). These populations were the Little Book Cliffs Wild Horse Range in Colorado, McCullough Peaks Herd Management Area in Wyoming, and Pryor Mountain Wild Horse Range in Montana; the research effort included over 1,800 hours of behavioral observations of 317 adult free-roaming feral horses. The following ethogram was developed during the course of this study to facilitate accurate scientific data collection on feral horse behavior, which is often challenging to quantify. By developing this set of discrete behavioral definitions and a set of strict research protocols, scientists were better able to address both applied questions, such as behavioral changes related to fertility control, and theoretical questions, such as understanding social networks and dominance hierarchies within social groups of equids.

Background

Feral horses in North America are descendents of animals that escaped domesticity or were intentionally released by settlers, explorers, and military personnel, and because of their highly adaptive nature were able to thrive in a multitude of environments. In the United States most feral horses are federally protected by the Wild Free-Roaming Horses and Burros Act of 1971, which refers to them as "living symbols of the historic and pioneer spirit of the West," stating that "they contribute to the diversity of life forms within the Nation and enrich the lives of the American people" (Public Law 92-195, 85 Stat. 649, as amended). Roughly 30,000 feral horses are distributed across 10 western States in the United States on 21.4 million ha of federally designated horse range. With annual population growth rates reported at 15–25 percent (Eberhardt and others, 1982; Wolfe and others, 1989; Garrott and Taylor, 1990; Garrott and others, 1991) and very limited natural depredation, the influence of feral horses on native flora, fauna, and ecosystem processes varies greatly (see Smith, 1986; Fahnestock and Detling, 1999; Coughenour, 2002; Levin and others, 2002; Beever and Herrick, 2006; Beever and others, 2008). 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). Additionally, when management practices such as fertility control alter natural biological processes, it is important to consider the ethical implications, such as influences on animal behavior and social structure (Nettles, 1997; Asa and others, 2005; Porton, 2005).

Social Organization

Feral horses arrange themselves in family groups known as bands, which range in size from 2 to 20 or more animals. Band size is variable and may be a response to both the environment the horses inhabit and population density. Animals can reduce risk of predation by living in groups (Pusey and Packer, 1997), and in open habitats without cover in which to hide, animals may form larger groups (Molvar and Bower, 1994). The latter was found to be true in the USGS study,

where mean band size in the sage steppe habitat found at McCullough Peaks was 8.01 ± 0.38 (SE) horses, while habitats with trees and dense vegetation had smaller mean band sizes—4.45 ± 0.16 horses at Little Book Cliffs and 4.16 ± 0.17 horses at Pryor Mountain.

Feral horse bands typically consist of a single polygynous stallion, adult females, foals of the year, and yearling males and females. Bands with multiple stallions do occur and were first reported by Denniston (1979) and Miller (1979). Miller (1979) found that multiple stallions were present only in bands consisting of greater than 9.3 horses. This finding was supported by the USGS study, during which multiple-stallion bands were recorded only at McCullough Peaks; multiple stallions occurred in five bands of horses consisting of 9–18 animals each. At 2 years of age, subordinate males typically disperse the band into bachelor groups of two to several horses, but occasionally 2- and 3-year-old males remain with the band if the stallion does not drive them away. Rutberg and Keiper (1993) found that the age at which male horse dispersal occurs is strongly correlated with the number of peers in the natal group.

Feral horse bands are not geographically territorial and home ranges overlap with those of other bands in the population. This geographically non-territorial, harem-type social structure is known as Type I organization and also is used by the Przewalski horse (*Equus ferus przewalskii*), Plains zebra (*Equus burchellii*), and Mountain zebra (*Equus zebra*) (Klingel, 1975; Rubenstein, 1989). The other organizational structure found in equids, Type II organization, involves adult males establishing geographic territories and females moving between them. Type II organization is used by the Grevy's zebra (*Equus grevyi*), African wild ass (*Equus africanus*), and Asiatic wild ass (*Equus hemionus*). While feral horses do not exhibit geographic territoriality, the USGS study did document resource-oriented territoriality whereby stallions (with the entire band present) defended mineral sources repeatedly and often with elevated agonistic interactions when other bands approached.

Ethological organization within horse bands is characterized by a dominance hierarchy, but the literature has conflicting functional explanations for hierarchical structures in equids. Houpt and others (1978) found that body weight affected social rank but age did not; however, other researchers (Keiper and Sambraus, 1986; Rho and others, 2004; Heitor and others, 2006) found age to be linearly correlated with social rank. Reproductive status of females has been shown to influence their social dominance in a band, as well as their rate of interchange between bands (van Dierendonck and others, 2004). Most studies, however, indicate that agonism is strongly correlated with dominance rank among females (Houpt and others, 1978; Waring, 1983; Keiper and Receveur, 1992; Weeks and others, 2000). The USGS study found that the most dominant members of feral horse bands were female, and stallion rank varied by band. This ethological structure is reported in much of the existing literature (Houpt and Keiper, 1982; McCort, 1984; Keiper and Sambraus, 1986; Klimov, 1988; and Keiper and Receveur, 1992). Lack of stallion dominance has been attributed to the amount of time stallions spend away from the band while recruiting new females or engaging in agonistic interactions with other stallions; females in a band, however, can establish stronger hierarchical relationships because they continuously remain in close proximity to one another (Keiper and Receveur, 1992). Social rank in bachelor groups, which are often unstable, has only been attributed to individual temperament (Tilson and others, 1988).

Ethological Data Collection and Analyses

It is possible to quantify behavior through the systematic enumeration of discretely defined categorical behaviors in terms of counts of occurrence or proportions of time exhibited. Collection of ethological data may be accomplished through several techniques, and the ultimate decision rests on the precisely defined research objectives. The reader is referred to Altmann (1974) for a definitive overview of sampling methodology for observational data. In the last 30 years, many insights have contributed to refining these methods, such as how to determine the appropriate time period between sampling when using the instantaneous scan sampling method and a better research design to capture infrequent behavioral expressions. In sampling feral horse behavior, the USGS study found that instantaneous scan sampling (the method of recording the categorical behavior of each focal animal at precise moments in time) at 1-min intervals was ideal for quantifying time budget data. Continuous sampling is an alternative to this technique and involves recording a focal animal's behavior continuously and noting the point in time that a new behavior begins. Continuous sampling was impractical for our study due to the number of animals and observers involved. Mitlohner and others (2001) found no significant difference between behavioral data recorded with instantaneous scan sampling versus continuous sampling when intervals were 15 minutes or less, and found a high correlation between the techniques when using 1-min intervals.

Collecting data on time budgets using instantaneous scan sampling is fairly straightforward, but behaviors that are infrequent and expressed briefly are not likely to be captured adequately (Houpt, 1991; Doran, 1992). Two relatively good options exist for collection of such data: the all-occurrence method and focal sampling. All-occurrence data collection records every behavior every time it is observed (Altmann, 1974) and can be a good technique when the number of animals in the focal band is not too large and the behaviors of interest are easy to detect. Although less efficient in terms of data collection, the focal sample method may be more reliable since the observer's focus is directed at only one animal (Altmann, 1974; Houpt, 1991). This method involves randomly selecting one individual in the band and continuously observing and recording all behavioral expressions. In feral

horse research, capturing briefly occurring expressions is most important for reproductive, social, and agonistic behaviors. Feeding, resting, and locomotion typically occur in periods long enough to be captured by most techniques.

Ethological protocols must be established prior to data collection and should be defined by research objectives. The discrete behavioral categories presented in this ethogram do not preclude the exhibition of simultaneous behaviors. For example, it is typical in feral horses for a comfort behavior such as masturbation to occur while the animal is feeding, so a protocol should be explicitly defined stating which behavior takes precedence in the data record. If the objective of your research is to determine the amount of time horses are feeding in relation to some covariate, then feeding is the appropriate category, and if expression of comfort behavior is the focus, then it should be recorded as such (or in this case, one might wish to subdivide comfort into several behaviors, since comfort is generally a short-duration behavior with many specific expressions). Regardless of the approach, notations of simultaneous occurrences are invaluable in retrospect.

Simultaneous behavioral expressions are not the only observational data collection pitfall. Some behaviors, such as olfactory investigation, can be ascribed to several categories. This behavior may fall under comfort, reproduction, or harem social behavior, but the correct categorization of such expressions is not subjective: each expression does have an absolute definition. In such cases, the context of the behavior will define its true characterization. When such potentially confusing behaviors are prevalent, they are addressed specifically in the ethogram.

Considerably more in-depth analyses of behavior are possible when covariates associated with individual focal subjects are collected reliably. Many factors may influence behavior, such as age, body condition, dominance rank, presence of dependent foal, climate, and habitat. Fortunately, many feral horses have unique natural markings, making identification of individual animals possible without the use of radio-collars or numbered tags. Pelage color; facial patterns such as snips, strips, blazes, and stars; and leg markings such as coronet bands, socks, and stockings collectively make cataloging and referencing study animals feasible (Sponenberg and Beaver, 1992; Gower, 2000; Green 2001). Properly cataloging and identifying individual horses in a research effort can provide the foundation from which to build in-depth covariate data and thus lead to a better understanding of animal behavior.

Analyses of behavioral data may incorporate many traditional statistical methods, but time budget data presents a particularly challenging dilemma. These analyses must consider the compositional nature of a time budget: models exhibiting strong support for one behavioral category must also be considered for each other category. Proportions of time spent in behavioral categories are compositional dependent variables because the sum of the proportions in all behavioral categories sum to 1. In other words, there is a unit sum constraint (Aitchison, 1986) by which more time spent in one or more behavioral categories must be associated with less time spent in one or more other behavioral categories. These compensatory shifts in estimates are absolute, leading to a dependent relationship among behaviors constituting the time budget being analyzed (Elston and others, 1996). Many compositional data-analysis procedures have been developed (for example, log-ratio procedures; Aitchison, 1986, 1992), but few are appropriate for data that exhibit real values of 0 or 1. It may be important that the amount of time an animal exhibits a given behavior is truly 0 percent or 100 percent. Many methods, such as log-ratio analysis, require data transformations that eliminate values of 0 and 1 by assigning very small or very large values (greater than 0 or less than 1) (Bakeman and others, 1992; Clark and Messina, 1998). This process ultimately alters the distribution of data and may adversely affect conclusions drawn about individual behaviors in the composition (Bingham and Brennan, 2004). Once transformed, the common method of log-ratio analysis also produces only quantitative statements about the overall distribution of the composition in comparison to another and the sampling distribution of the difference; it does not specify explicit contributions of each piece of the composition to those differences (Aitchison, 1986). If your data are not composed of real values of 0 and 1, log-ratio analyses may be appropriate. It is best suited for compositions with only two elements since conclusions about the change in allocation may be drawn easily (Elston and others, 1996), but most behavioral studies aim to address multiple behaviors. Some extensions of the algebra of log-ratio compositional measures have been made by Billheimer and others (2001), but currently these procedures are limited to three-part compositions and still suffer the restriction of not allowing zero proportions.

One solution to the problem of comparing time-budget compositions with several behaviors and true values of 0 and 1 is the use of a multi-response permutation procedure (MRPP; Mielke and Berry, 2007). This method does not require data-transformation and analyzes compositional differences by approximating probabilities of a test statistic based on average Euclidean distances for detecting distributional differences. In other words, the test is focused on differences in multivariate cumulative distributions rather than means. This approach may yield useful results for drawing conclusions about how different animals or treatment groups allocate their time, but it still does not provide insightful conclusions about specific behaviors within the composition of interest. No standardized way to approach this problem currently exists, but one solution is simply to model each behavior to query further covariates and relationships of interest: analyze each part of the behavioral composition as a univariate dependent variable. For such results to be interpretable, however, the same models must be applied and presented for all individual behaviors in the composition.

In simple compositions with few behaviors, the trade-off in time allocation may be evident. It is likely, however, that such clear trade-offs will not always be evident and multiple models must be presented for each behavior. For example, consider a simple composition of three horse behaviors

(Y_f = feeding, Y_r = resting, and Y_l = locomotion, where $Y_f + Y_r + Y_l = 1.0$). If Y_f has a strong linear increase with the predictor variable X_1 (for example, 0/1 indicator variable of sex) and a weak linear increase with predictor variable X_2 (for example, herd size), then Y_r, Y_l, or both must decrease with X_1, but the actual magnitude of that decrease will depend on both behaviors and the degree to which they also are influenced by X_2 (model 1 is $Y = f(X_1 + X_2)$). It could easily be that the strongest model for Y_r might include X_2 and another predictor (say X_3, and model 2 is $Y = f(X_1 + X_3)$). Thus, it is possible for model 1 to be strongly selected for analyzing the Y_f part of the Y compositional vector of behaviors but model 2 to be strongly selected for the Y_r part of the composition. Likewise, one model may be strongly supported for several behaviors and a complement model may be strongly supported for the remaining behaviors in the composition (see Ransom, 2009); however, because the behavioral composition really induces a relationship among the parts of the composition, statistical model results will be uninterpretable if a selected model is not considered to apply to all parts of the behavioral composition (for example, Y_f, Y_r, and Y_l).

The increasing use of maximum-likelihood and Bayesian approaches for solving complex problems may ultimately lead to the development of more lucid guidelines for many problems indicative of behavioral data. These methods can provide powerful tools for analyzing scientific data and can lead to a deeper understanding of the processes and errors involved (Hobbs and Hilborn, 2006). Regardless of the statistical approach, the path toward proper model selection for individual dependent behaviors in a composition has not been described in the literature. The use of model weights and model averaging may assist in drawing coherent conclusions about parameters of interest (Burnham and Anderson, 2002), but all supported models must be considered simultaneously for all dependent compositional variables to avoid violating the inherent statistical assumptions. A reasonable approach to assessing strength of evidence for compositional models, without violating assumptions of dependence, is to sum the minimum Akaike's Information Criteria (AIC: Burnham and Anderson, 2002) scores for the individually-modeled constituent behaviors in a composition; subsequently, each sum then forms an aggregate AIC score for each compositional model. The strength of evidence for the overall composition may then be assessed using AIC weights as Burnham and Anderson (2002) describe for individual models.

Ethogram

This ethogram was developed to investigate the influences of fertility control on feral horse behavior; thus, the behavioral groupings are broad in some contexts, such as feeding behavior, and much more detailed in areas of specific interest to the research objectives, such as agonism. Behavioral researchers often consolidate an array of behavioral expressions into broad categories since data collection on every specific behavior expressed is usually impractical and makes analyses excessively difficult. Therefore, this ethogram divides behavioral expressions into 13 discrete categories that cover the range of expressions a feral horse may exhibit in free-roaming conditions. Two additional categories (human awareness and out-of-sight) are used to account for biased observations. These 13 categories can easily be further aggregated *a posteriori* if desired, but categorizing these behaviors separately *a priori* allows for a wider range of possible analyses while still being practical for data collection. An example of a broader aggregation of these categories is the consolidation of grooming, comfort, standing attentive, and elimination into *maintenance*; herding, reproduction, harem tending, harem social, agonism, and submission into *social*; and human awareness and out-of-sight (unavailable to the observer) into *unknown* (fig. 1). At any given time during the course of observation, a focal animal will be exhibiting behavior that can be described by one of these categories. Developing a research ethogram from the several hundred behavioral expressions documented in equids can be a daunting task; therefore, this basic ethogram for feral horses is presented as a starting point for behavioral studies. For an excellent ethogram resource detailing complete equid behavior expressions, the reader is referred to McDonnell (2003). For a comprehensive work on equine behavior, the reader should also see Waring (1983).

Feeding

Feeding behavior occupies roughly half of the daily time budget of feral horses (fig. 1) and usually entails grazing. Grazing occurs as a horse bites off and ingests grasses and forbs close to the ground (fig. 2). The feeding category also includes browsing on woody plants and trees, eating snow, drinking, mineral licking, coprophagy (eating feces), and pawing at food resources. The latter is critical in defining feeding as a mutually exclusive category in that a horse may be pawing at soil, plants, or snow, but if the action is directly related to acquiring and ingesting a food resource, then it should be considered as feeding behavior. Also, horses move as they graze; therefore, as long as the horse is feeding while it is moving, it should be considered as feeding rather than locomotion.

Resting

The second largest amount of time in the daily time budget of feral horses is allocated to resting, which may occur during 25–35 percent of the daylight hours (fig. 1). Resting behavior is characterized by a general lack of attention and relaxed state and may occur in a standing position or in recumbency (fig. 3). This includes both relaxation and sleeping. Horses are able to sleep standing up due to the stay apparatus that allows their body to be supported without active muscular control (Dallaire, 1986). This behavior is typically observed

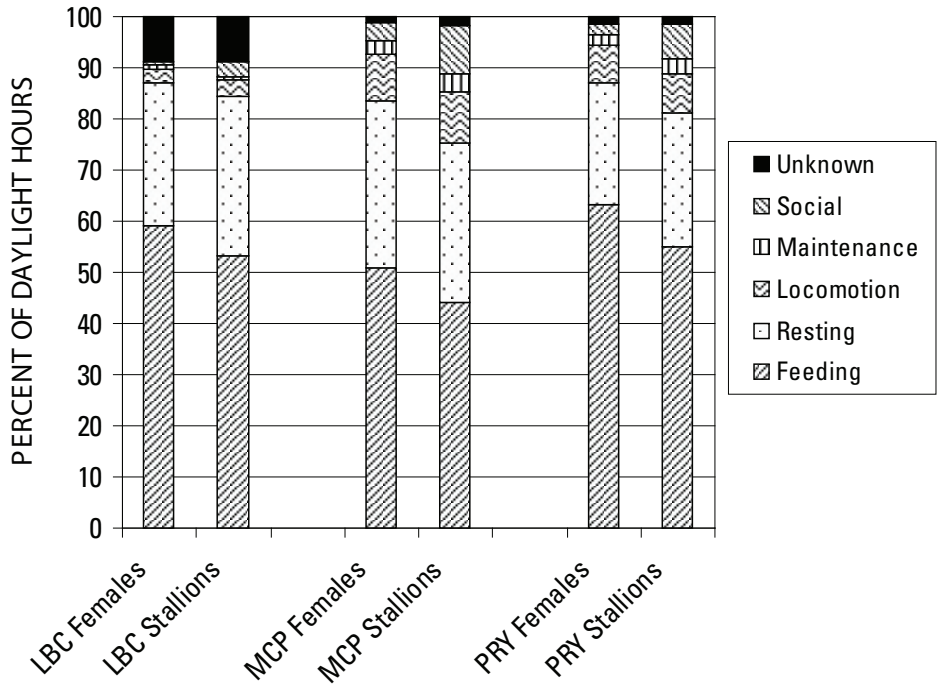

Figure 1. Observed daytime activity budgets of adult control female feral horses (n = 207, mean age = 7.79 yrs ± 0.33 SE, range = 2–21 yrs) and harem stallions (n = 110, mean age = 11.63 yrs ± 0.43 SE, range = 5–26 yrs) at Little Book Cliffs Wild Horse Range in Colorado (LBC), McCullough Peaks Herd Management Area in Wyoming (MCP), and Pryor Mountain Wild Horse Range in Montana (PRY), 2003–2006.

Figure 2. Feral horses grazing, the most typical *feeding* behavior.

Figure 3. *Resting* behavior in a band of feral horses is often characterized by huddling. Aside from the physical protection received by this behavior, the head-to-tail orientation of band members in this type of resting behavior also facilitates grooming. This allows for insect control around the head by the tail-swishing effect of neighbors.

as a body position with the head lowered, eyes closed, and one rear foot slightly elevated. Resting behavior in a band is often characterized by huddling, which facilitates insect control by the tail-swishing of close neighbors. Recumbent rest can be sternal or lateral. The comfort behavior of sun-basking is expressed in a laterally recumbent state, so a protocol must be defined *a priori* characterizing this state as rest or comfort, based on research objectives.

Locomotion

The third largest amount of the daily time budget is spent on locomotion. This behavior includes walking, trotting, cantering, galloping, jumping, and swimming and in feral horses is typically used for moving from one resource to another (fig. 4). Since most feral horse populations in North America occupy arid or semi-arid environments, movement to the few and scattered water sources is often the impetus for daily occurrences of extended locomotion (typically every 12 to 24 hrs). Otherwise, feral horses do not expend vast amounts of energy in locomotion, with the exceptions of brief social interactions between bands, stallion agonistic expressions, and female recruitment efforts by stallions. In this ethogram, locomotion integral to reproductive, harem tending, or comfort behaviors is considered part of its respective behavioral expression and not recorded as locomotion.

Maintenance

Grooming

Grooming behavior occupies a relatively small but important part of the daily time budget of feral horses and is often observed as rolling. Rolling occurs both on land and in water and is thought to assist with pelage health and insect control (fig. 5) (Waring, 1983). Other grooming behaviors include shaking, nibbling or licking on self, tail-swishing, rubbing, and periodic stomping to displace flies and biting insects. Allogrooming (also known as mutual grooming) in this ethogram is not considered categorically as a grooming behavior since it is also a social interaction that involves more than one animal. Depending on the nature of the research, it may be appropriate to consider allogrooming as part of the grooming category.

Figure 4. *Locomotion* is most typically expressed as walking from one place to another, as seen in this feral horse stallion. The higher energy-expense gaits of trotting, cantering, and galloping are observed far less frequently.

Figure 5. *Rolling* by this feral horse mare is a grooming behavior associated with pelage hygiene and insect control.

Comfort

Comfort behavior takes on a wide variety of forms in feral horses and includes any type of self-enjoyment expression, such as play, investigation, and stimulation (fig. 6). Some examples of comfort behavior are sun-basking, shelter seeking, masturbation, sexual play, object play, locomotor play, play fighting, and some olfactory investigations. Olfactory investigations also may be indicative of reproductive behavior or social behavior and should be included in the appropriate category for data collection based on specific research objectives. This ethogram also includes yawning and stretching as comfort behaviors, though it would not be inappropriate to include those expressions as a form of resting behavior.

Standing Attentive

When horses receive a stimulus that causes alertness, they react by exhibiting a rigid body posture with head upright, ears pointed forward, and eyes open and alert (fig. 7). This may be momentary in the case of a sound or smell causing alertness, but such standing attentive behavior also occurs for extended periods of time when a female is standing guard over a sleeping foal or a predator is nearby. In this ethogram, standing attentive does not include instances when the behavior is a result of human presence (fig. 8). In those cases, human awareness is considered its own category so that the biased data may be properly addressed during analyses.

Elimination

Elimination in horses is expressed as urination or defecation (fig. 9), though depending on research objectives, it should be determined whether any such expression will be included in this category or whether elimination with social implications is considered elsewhere. Socially, feral horse stallions create fecal middens known as stud piles and repeatedly defecate on them. These middens are thought to facilitate communication or ownership status of certain resources (Feist and McCullough, 1976; Rubenstein and Hack, 1992). When female feral horses urinate or defecate, it is common for the harem stallion to cover it with his urine for similar reasons. It has been reported that female horses do not cover the urine of other females in this fashion (McDonnell, 2003), though this was documented periodically during our study and may have implications in the female dominance hierarchy.

Figure 6. A typical *comfort* behavior for feral horse males is masturbation, which is expressed when a horse flexes his erect penis against his abdomen. This behavior is not expressed in conjunction with a nearby female and should not be confused with the penis drop observed when a male is reproductively tending a female.

Figure 7. Feral horse mares are focused on an external stimulus (in this case, a foal distress vocalization in the distance) and are exhibiting *standing attentive* behavior. Note the directionally pointed ears, rigid body position, and focused eyes characteristic of this expression. This behavior should not be confused with *human awareness*.

Figure 8. *Human awareness* is an important behavior to record when conducting any behavioral research so that biased data can be properly omitted from analyses of naturally occurring behaviors. Here, an entire band has paused because they noticed the photographer in the distance.

Figure 9. A female feral horse is exhibiting *elimination* by urination. Urination behavior in horses is sexually dimorphic: female horses urinate in a posterior direction and male horses urinate in an anterior direction.

In this ethogram, random urination and defecation are considered elimination, whereas systematic covering of urine or feces from the female by a harem stallion is considered as a harem tending behavior. The systematic covering of urine from a female by a female in the same harem is considered harem social behavior.

Social

Harem Social

Harem social behavior is considered to be social interaction among band members that is not specifically indicative of reproductive, harem tending, or agonistic behavior. Allogrooming is considered a harem social behavior in this ethogram (fig. 10), as is olfactory investigation (from one horse to another, fig. 11, or the systematic smelling of urine deposits among band members) and pair-bonding among juveniles (fig. 12).

Herding

When a feral horse stallion actively drives females of his harem together, it is considered herding behavior. This involves the stallion moving systematically behind the females, posturing with his head held low and ears laid back, and controlling the direction and movement of the band members (fig. 13). Waring (1983) termed this motion with the stallion's head moving side-to-side as snaking. Some researchers may choose to consider this as an agonistic behavior, but it is considered here as its own category since the function of the behavior is maintaining the harem rather than aggression toward specific females.

Harem Tending

Harem tending consists of stallion behaviors that are directed at maintaining the harem and include the defense and recruitment of females. The defense of females is expressed as a stallion positioning himself between his harem females and a perceived threat (typically another stallion) (fig. 14). It is also expressed by covering a female's urine or feces with his own, or by depositing feces on a stud pile (fig. 15). Recruitment, or stealing, of females by a harem stallion from another stallion is also considered harem tending behavior in this ethogram.

Reproduction

Reproductive behavior in feral horses is characterized by a series of stallion-initiated behaviors and a series of mare-initiated behaviors. The stallion reproductive sequence often

Figure 10. One of the most common *harem social* behaviors is allogrooming (also known as mutual grooming). It is expressed by the lateral parallel body position of two horses that allows for nibbling along the back or withers of each horse. While this behavior can be considered grooming, it is also thought to facilitate pair-bonding and dominance structure between band mates (Waring, 1983).

Figure 11. Olfactory investigation in the *harem social* behavior context is often observed as prolonged olfactory engagement of a female and her foal in a bonding regimen. This also may include licking and nudging.

Figure 12. Pair-bonding among juveniles within a band is also a common *harem social* behavior. In this example, female foals are closely engaging each other, which is thought to facilitate development of the female-female ethological relationships critical to band structure and stability later experienced as reproductive members of a family group (Crowell-Davis and others, 1986).

Figure 13. A feral horse stallion (leftmost horse) is *herding* females in his band by posturing and actively driving his females back into a cohesive group. Herding is the most common social behavior expressed by the dominant male toward females in his harem.

Figure 14. The blue roan stallion (foremost) is *harem tending* by expressing a posturing behavior and positioning himself between his harem females (several additional females out of the photo to the left) and an intruding male (right). Depending on the persistence and signals of the intruder, this behavior may develop into *agonism*.

Figure 15. Male feral horses also express *harem tending* by maintaining fecal middens, or stud piles, in which feces are aggregated at strategically located positions within the band's home range.

(but not always) begins with herding or reproductive tending behavior. Reproductive tending is the close following of a female by the male, without the directional driving observed in herding behavior. Following this tending behavior, the stallion often vocalizes and exhibits the olfactory response known as flehmen (fig. 16) (Stahlbaum and Houpt, 1989). He then proceeds by rubbing his head on the female's flanks and (or) resting his chin on her back, and extends his penis out of the prepuce (fig. 17). Some of these behaviors out of sequence are not necessarily associated with a stallion reproductive sequence; therefore, protocols to determine how to categorize the observed behavior are specified in figure 18.

Female reproductive behavior is signified by estrous, which can sometimes be challenging to detect from typical field observation distances. A mare initiates her reproductive sequence by presenting herself facing away from the stallion, lifting her tail, and vocalizing (though sometimes the female faces the stallion first). These behaviors alone do not necessarily signify estrous, since the female could simply be vocalizing and preparing to defecate. If in estrous, it is typically accompanied by posturing her body with hind legs slightly apart (an apparent squat) and often turning her head toward her posterior. The mare also will frequently emit small streams of urine, a behaviour that is often concurrent with rhythmic 'winking' of her vulva: winking can be observed by the periodic flashes of pink from the inner coloration of her vaginal membranes (McDonnell, 2003). These contrasting pigments can be seen in the rolling female in figure 5, simply because of her posture. The urine emitted from female horses in estrous consists of specific variations of urinary volatile compounds that may facilitate chemical communication during reproductive behavior (Ma and Klemm, 1997). Female horses may express estrous behavior during the anovulatory period (typically winter) as well as during pregnancy (Crowell-Davis, 2007). Such anomalies to our conventional understanding may lead to misinterpretation of estrous behavior in the field and care should be taken to correctly and systematically identify this behavior.

Once both male and female are exhibiting reproductive behaviors, copulation may occur with the stallion mounting the female from behind, neck arched over her back and forelegs resting on her sides (fig. 19). Several events could occur in this situation and should be categorized separately if reproductive behavior is a focus of the research. These include successful copulation, unsuccessful copulation (the stallion cannot adequately mount the female for some reason), mare acceptance, mare rejection (the mare kicks and moves away from the stallion), and forced copulation (the mare is not presenting or accepting the stallion's advance, but he relentlessly mounts her anyway).

Figure 16. Flehmen response in this feral horse stallion is displayed by the elevated head, and raised, inverted upper lip. This posture is a response to particularly exciting chemicals and olfactory signals that are detected by the main olfactory epithelium and concentrated directly into the vomeronasal organ, which in part controls sexual activity (Estes, 1972; Mills and Nankervis, 1999).

Figure 17. A feral horse stallion is exhibiting penis extension and rubbing of the female's flanks as part of the male reproductive behavior sequence.

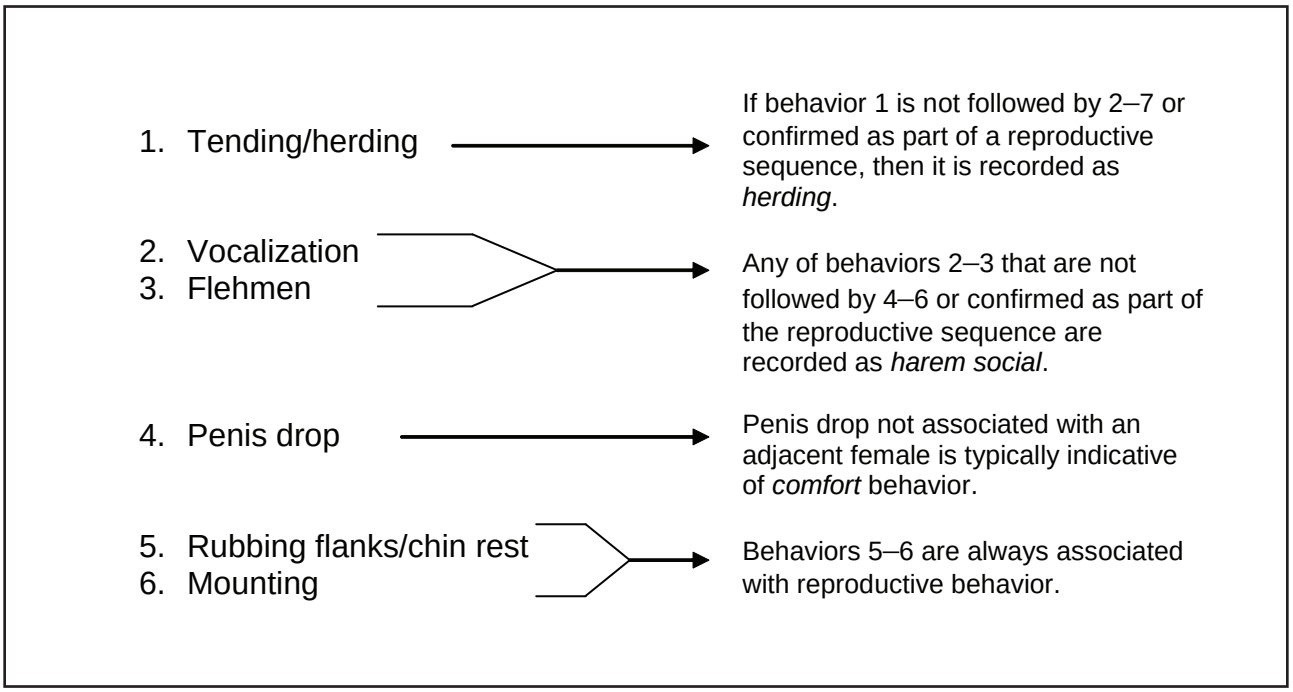

Figure 18. Basic guidelines for distinguishing reproductive and non-reproductive behaviors in stallions.

Figure 19. *Successful copulation* is occurring between this feral horse male and female. This reproductive behavior is characterized by a maintained mounting position on the female for the male and a relatively stationary, relaxed position for the female. *Unsuccessful copulation* is often a result of *mare rejection*, with the female expressing *agonistic* behaviors such as kicking toward the male and a brief mounting position for the male.

Parturition may also be included in the reproductive category or designated as its own behavioral category, depending on research focus.

Agonism

Agonism in feral horses is exhibited by a wide range of behaviors and in this ethogram is put into seven categories arranged by increasing intensity of the interaction. Note that any or all of the following behaviors may be exhibited in play by young animals, in which case they should be considered comfort behavior rather than agonism. The first four categories of agonism may occur between males only, females only, or between males and females, but the remaining levels of agonism are typically observed only between males.

1. The most common and least intense form of agonism is the threat. Threats are characterized by laterally pinned back ears, arched neck, and (or) a movement of the head toward the opposing horse, but with no physical contact (fig. 20). Most conflicts and dominance interactions among feral horses are resolved by these gestures alone.

2. The next agonistic expression is the bump or push, which is expressed by the aggressor making forceful contact with another horse using its head, neck, or shoulder (fig. 21).

3. As agonism escalates, the aggressor may chase its adversary at a gallop to displace the animal from the immediate area or with the intent of engaging the animal in more agonistic behavior (fig. 22). Chasing behavior is typically brief (seconds) or may last several minutes; however, the USGS study documented this behavior occasionally persisting over long time periods (greater than 1 hour) and great distances (greater than 3 km).

4. The fourth level of agonism involves biting an opponent or kicking with the hind legs (fig. 23). This level involves physical contact, though serious injury is rare.

5. Rearing occurs when the horse lifts its forelegs off the ground and elevates its body into a more vertical position, thus looking larger to the opponent (fig. 24). While technically only a threat, this body position typically signifies a more intense agonistic interaction and provides the initial position for commencement of stomping, striking, boxing, and dancing behaviors.

Figure 20. *Agonism* is expressed by both of these feral horses in the form of a *threat*. This is the most common form of agonism between feral horses and is most easily recognized by the laterally positioned, posterior pointing direction of the ears (shown in both animals here).

Figure 21. *Pushing* is an agonistic expression shown here by the foremost horse pushing toward the more distant horse.

Figure 22. *Chasing* is a moderately intense form of agonism and is shown here along with an expression of imminent biting behavior.

Figure 23. *Biting* is a common expression of agonism in equids and is expressed here between feral horse females to assert dominance.

Figure 24. *Rearing* is an expression often signifying a potentially intense agonistic interaction, typically between feral horse stallions.

Figure 25. *Striking* or *stomping* is being expressed by the feral horse stallion on the left. This behavior is typically indicative of highly agonistic expression and is expressed by the directed extension and downward motion of one or both front feet.

6. Stomping and striking occur when a horse uses one or both front feet to attack an opponent by extending the legs out and downward. This behavior has the potential to seriously injure the recipient (fig. 25).

7. The most intense form of agonism between feral horse stallions is boxing and dancing. These behaviors involve the engagement of the agonists in vertical body positions and the use of the front legs in striking (boxing) or closer engagement that results in head and neck biting (dancing) (fig. 26). On very rare occasions, feral horse stallions have been observed engaging in prolonged fights resulting in considerable injury and sometimes fatal outcomes.

Submission

Submission is exhibited by the loser of the agonistic encounter. This may be expressed by simply running away, but also may be expressed with laid down ears (distally or posteriorly), lowered head posture, lowering of the hindquarters, and sometimes jaw snapping (especially in juveniles) (fig. 27).

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Figure 26. *Boxing* and *dancing* between these two stallions is illustrative of the highest level of agonism that feral horses typically express.

Figure 27. *Submission* is being expressed by a young male horse (grullo [dark grey] horse in center) and directed toward the larger, dominant male (foremost), who is displaying *threat* behavior associated with dominance.

References

Aitchison, J., 1986, The statistical analysis of compositional data (with discussion): Journal of the Royal Statistical Society (B), v. 44, p. 1,313–1,325.

Aitchison, J., 1992, On criteria for measures of compositional difference: Mathematical Geology, v. 24, p. 365–379.

Altmann, J., 1974, Observational study of behavior—Sampling techniques: Behaviour, v. 49, p. 227–267.

Asa, C.S., Porton, I.J., and Calle, P.P., 2005, Choosing an appropriate contraceptive, *in* Asa, C.S., and Porton, I.J., eds., Wildlife contraception: Baltimore, Md., Johns Hokpins University Press, p. 83–95.

Bakeman, R., Forthman, D.L., and Perkins, L.A., 1992, Time-budget data—Log-linear and analysis of variance compared: Zoo Biology, v. 11, p. 271–284.

Beever, E.A., and Herrick, J.E., 2006, Effects of feral horses in Great Basin landscapes on soil and ants—Direct and indirect mechanisms: Journal of Arid Environments, v. 66, n. 1, p. 96–112.

Beever, E.A., Tausch, R.J., and Thogmartin W.E., 2008, Multi-scale responses of vegetation to removal and horse grazing from Great Basin (USA) mountain ranges: Plant Ecology, v. 196, n. 2, p. 163–184.

Billheimer, D., Guttorp, P., and Fagan, W.F., 2001, Statistical interpretation of species composition: Journal of the American Statistical Association, v. 96, n. 456, p. 1,205–1,214.

Bingham, R.L., and Brennan, L.A., 2004, Comparison of type I error rates for statistical analyses of resource selection: Journal of Wildlife Biology, v. 68, n. 1, p. 206–212.

Buchholz, R., 2007, Behavioural biology—An effective and relevant conservation tool: Trends in Ecology and Evolution, v. 22, n. 8, p. 401–407.

Burnham, K.P., and Anderson, D.R., 2002, Model selection and multimodel inference—A practical-theoretic approach (2d ed.): New York, Springer Publishing, 488 p.

Clark, T.L., and Messina, F.J., 1998, Plant architecture and the foraging success of ladybird beetles attacking Russian wheat aphid: Entomology Experimental Applications, v. 86, p. 153–161.

Coughenour, M., 2002, Ecosystem modeling in support of the conservation of wild equids—The example of the Pryor Mountain Wild Horse Range, *in* Moehlman, P.D., ed., Equids—Zebras, asses, and horses. Status survey and conservation action plan, IUCN/SSC Equid Specialist Group: Gland, Switzerland, and Cambridge, U.K., International Union for Conservation of Nature, p. 154–162.

Crowell-Davis, S.L., 2007, Sexual behavior of mares: Hormones and Behavior, v. 52, p. 12–17.

Crowell-Davis, S.L., Houpt, K.A., and Carini, C.M., 1986, Mutual grooming and nearest-neighbor relationships among foals of *Equus caballus*: Applied Animal Behaviour Science, v. 15, p. 113–123.

Dallaire, A., 1986, Rest behavior, *in* Crowell-Davis, S.L., and Houpt, K.A., eds., The veterinary clinics of North America, equine behavior: Philadelphia, W.B. Saunders Co., p. 591–607.

Denniston, R.H., 1979, The varying role of the male in feral horses, *in* Symposium on the ecology and behavior of wild and feral equids, Laramie, Wyo., 6–8 September 1979, Proceedings: Laramie, Wyo., University of Wyoming, p. 93–98.

Doran, D., 1992, Comparison of instantaneous and locomotor bout sampling methods—A case study of adult male chimpanzee locomotor behavior and substrate use: American Journal of Physical Anthropology, v. 89, p. 85–99.

Eberhardt, L.L., Majorowicz, A.K., and Wilcox, J.A., 1982, Apparent rates of increase for two feral horse herds: Journal of Wildlife Management, v. 46, p. 367–374.

Elston, D.A., Illius, A.W., and Gordon, I.J., 1996, Assessment of preference among a range of options using log ratio analysis: Ecology, v. 77, n. 8, p. 2,538–2,548.

Estes, R.D., 1972, The role of the vomeronasal organ in mammalian reproduction: Mammalia, v. 36, p. 315–341.

Fahnestock, J.T., and Detling, J.K.,1999, The influence of herbivory on plant cover and species composition in the Pryor Mountain Wild Horse Range, USA: Plant Ecology, v. 144, p. 145–157.

Feist, J.D., and McCullough, D.R., 1976, Behavior patterns and communication in feral horses: Zeitschrift für Tierpsychologie, v. 41, n. 4, p. 337–371.

Garrott, R.A., Siniff, D.B., and Eberhardt, L.L., 1991, Growth rates of feral horse populations: Journal of Wildlife Management, v. 55, p. 641–648.

Garrott, R.A., and Taylor, L., 1990, Dynamics of a feral horse population in Montana: Journal of Wildlife Management, v. 54, p. 603–612.

Gower, J., 2000, Horse color explained: North Pomfret, Vt., Trafalgar Square Publishing, 144 p.

Green, B.K., 2001, The color of horses—The scientific and authoritative identification of the color of the horse: Missoula, Mont., Montana Press Publishing, 127 p.

Heitor, F., Oom, M.M., and Vicente, L., 2006, Spatial relationships in a herd of Sorraia horses. Part I. Correlates of social dominance and contexts of aggression: Behavioural Processes, v. 73, p. 170–177.

Hobbs, N.T., and Hilborn, R., 2006, Alternatives to statistical hypothesis testing in ecology—A guide to self teaching: Ecological Applications, v. 16, n. 1, p. 5–19.

Houpt, K.A., 1991, Investigating equine ingestive, maternal, and sexual behavior in the field and in the laboratory: Journal of Animal Science, v. 69, p. 4,161–4,166.

Houpt, K.A., and Keiper, R., 1982, The position of the stallion in the equine dominance hierarchy of feral and domestic ponies: Journal of Animal Science, v. 54, n. 5, p. 945–950.

Houpt, K.A., Law, K., and Martinisi, V., 1978, Dominance hierarchies in domestic horses: Applied Animal Ethology, v. 4, p. 273–283.

Keiper, R., and Receveur, H., 1992, Social interactions of free-ranging Przewalski horses in semi-reserves in the Netherlands: Applied Animal Behaviour Science, v. 33, p. 303–318.

Keiper, R.R., and Sambraus, H.H., 1986, The stability of equine dominance hierarchies and the effects of kinship, proximity and foaling status on hierarchy rank: Applied Animal Behaviour Science, v. 16, n. 2, p. 121–130.

Klimov, V.V., 1988, Spatial-ethological organization of the herd of Przewalski horses (*Equus przewalskii*) in Askania-Nova: Applied Animal Behaviour Science, v. 21, p. 99–115.

Klingel, H., 1975, Social organization and reproduction in equids: Journal of Reproduction and Fertility, Supplement 23, p.7–11.

Levin, P.S., Ellis, J., Petrik, R., and Hay, M.E., 2002, Indirect effects of feral horses on estuarine communities: Conservation Biology, v. 16, n. 5, p. 1,364–1,371.

Ma, W., and Klemm, W.R., 1997, Variations in equine urinary volatile compounds during the oestrous cycle: Veterinary Research Communications, v. 21, p. 437–446.

McCort, W.D., 1984, Behavior of feral horses and ponies: Journal of Animal Science, v. 58, n. 2, p. 493–499.

McDonnell, S., 2003, A practical field guide to horse behavior—The equid ethogram: Lexington, Ky., The Blood Horse, Inc., 375 p.

Mielke, P.W., Jr., and Berry, K.J., 2007, Permutation methods—A distance function approach (2d ed.): New York, Springer Publishing, 439 p.

Miller, R., 1979, Band organization and stability in Red Desert feral horses in Symposium on the ecology and behavior of wild and feral equids, Laramie, Wyo., 6–8 September 1979, Proceedings: Laramie, Wyo., University of Wyoming, p.113–128.

Mills, D., and Nankervis, K., 1999, Equine behaviour—Principles and practice: Malden, Mass., Blackwell Science, 232 p.

Mitlohner, F.M., Morrow-Tesch, J.L., Wilson, S.C., Dailey, J.W., and McGlone, J.J., 2001, Behavioral sampling techniques for feedlot cattle: Journal of Animal Sciences, v. 79, n. 5, p.1,189–1,193.

Molvar, E.M., and Bower, R.T., 1994, Costs and benefits of group living in a recently social ungulate— The Alaskan moose: Journal of Mammalogy, v. 75, n. 3, p. 621–630.

Nettles, V.F., 1997, Potential consequences and problems with wildlife contraceptives: Reproduction, Fertility, and Development, v. 9, p.137–143.

Porton, I.J., 2005, The ethics of wildlife contraception, *in* Asa, C.S., and Porton, I.J., eds., Wildlife contraception: Baltimore, Md., Johns Hopkins University Press, p. 3–16.

Pusey, A.E., and Packer, C., 1997, The ecology of relationships, *in* Krebs, J.R., and Davies, N.B., eds., Behavioral ecology—An evolutionary approach: Malden, Mass., Blackwell Publishing, p. 254–283.

Ransom, J.I., 2009, Understanding the influences of immunocontraception on equids through competing models of behavior: Fort Collins, Colo., Colorado State University, M.S. thesis, 61 p.

Ransom, J.I., Swann, M.E., Wilson, J.T., and Roelle, J.E., 2007, America's wild horses and burros—Research for management: Fort Collins, Colo., U.S. Geological Survey Fort Collins Science Center, *http://www.fort.usgs.gov/wildhorsepopulations*, accessed November 2008.

Rho, J.R., Srygley, R.B., and Choe, J.C., 2004, Behavioral ecology of the Jeju pony (*Equus caballus*)—Effects of maternal age, maternal dominance hierarchy and foal age on mare aggression: Ecological Research, v. 19, n. 1, p. 55–63.

Rubenstein, D.I., 1989, Life history and social organization in arid adapted ungulates: Journal of Arid Environments, v. 17, p.145–156.

Rubenstein, D.I, and Hack, M.A., 1992, Horse signals—The sounds and scents of fury: Evolutionary Ecology, v. 6, p. 254–260.

Rutberg, A.T., and Keiper, R.R., 1993, Proximate causes of natal dispersal in feral ponies—Same sex differences: Animal Behaviour, v. 46, p. 969–975.

Smith, M.A., 1986, Impacts of feral horse grazing on rangelands—An overview: Journal of Equine Veterinary Science, v. 6, n. 5, p. 236–239.

Sponenberg, D.P., and Beaver, B.V., 1992, Horse color—A complete guide to horse coat colors: Ossining, N.Y., Breakthrough Publications, 124 p.

Stahlbaum, C.C., and Houpt, K.A.,1989, The role of flehmen response in the behavioural repertoire of the stallion: Physiology and Behavior, v. 45, p. 1,207–1,214.

Sutherland, W.J., 1998, The importance of behavioural studies in conservation biology: Animal Behaviour, v. 56, p. 801–809.

Tilson, R.L., Sweeny, K.A., Binczik, G.A., and Reindl, N.J., 1988, Buddies and bullies—Social structure of a bachelor group of Przewalski horses: Applied Animal Behaviour Science, v. 21, n. 1, p. 169–185.

van Dierendonck, M.C., Sigurjónsdóttir, H., Colenbrander, B., and Thorhallsdóttir, A.G., 2004, Differences in social behaviour between late pregnant, post-partum and barren mares in a herd of Icelandic horses: Applied Animal Behaviour Science, v. 89, p. 283–297.

Waring, G.H., 1983, Horse behavior: Park Ridge, N.J., Noyes Publications, 292 p.

Weeks, J.W., Crowell-Davis, S.L, Caudle, A.B., and Heusner, G.L., 2000, Aggression and social spacing in light horse (*Equus caballus*) mares and foals: Applied Animal Behaviour Science, v. 68, p. 319–337.

Wolfe, M.L., Ellis, L.C., MacMullen, R., 1989, Reproductive rates of feral horses and burros: Journal of Wildlife Management, v. 53, no. 4, p. 916–924.

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