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# Agonistic ethogram of the equid bachelor band

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## Abstract

An ethogram of agonistic and related behaviors among equid bachelor band members was developed. Several key English-language studies on equids were reviewed to derive a preliminary inventory of specific behaviors to be included in the ethogram. A bachelor band of domestic pony stallions pastured together was observed for approximately 50 daylight hours to obtain detailed descriptions of each behavior, enable photographic and video documentation of behaviors, and identify any behaviors to be added to the preliminary inventory. An initial draft of the ethogram was sent to 65 equine researchers for review. Twenty-eight critical reviews were received and their suggestions considered for the final draft.

A total of 49 elemental behaviors including five distinct vocalizations was included in the ethogram. Three complex behavioral sequences were also included. Most of the behaviors catalogued from the direct observation of pastured pony stallions were also found in the equid literature. For many, references to these behaviors specifically among males or bachelor band members were not found.

The results offer a practical tool for quantitative research and other studies of equid inter-male behavior as well as for teaching of equid behavior, and should facilitate progress toward development of a complete ethogram for the horse and other equids.

Keywords: Equid; Horse; Bachelor; Agonistic; Social behavior; Ethogram

# 1. Background and purpose

Equid behavior has historically been of great interest to animal keepers, biologists, animal scientists, veterinarians, and ethologists. Numerous descriptive accounts of equid behavior as well as a few systematic studies focusing on particular species or classes of behavior are available throughout the lay and scientific literature in several different languages. In this body of information, there are notable apparent inconsistencies in the terminology and interpretations of behavior.

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An ethogram is a formal list of a species' behavioral repertoire or a major segment of it (Grier, 1984, p. 56). It may be a complete list of all behaviors or it may focus on particular functional classes of behaviors (Grier, 1984, p. 69). The format may be a simple alphabetical listing of behaviors by name, or it may include detailed descriptive text and/or line drawings of behavioral elements or sequences, or pictorial representations of interactive sequences. To our knowledge, a complete equid ethogram has not been published. It is our long-range goal to prepare a concise, comprehensive equid ethogram, primarily for use in behavioral research.

Equid bachelor bands are relatively stable associations of non-breeding males. Among equids, which are all polygynous breeders, there are two distinct types of social organization (reviewed by Klingel, 1975). The domestic and feral donkeys, Grevy's zebra, and African and Asian asses are known as territorial breeders. The breeding stallions hold territories to which females travelling in association are attracted for breeding. The non-breeding males mingle among loosely associated mixed-sex herds where they may interact with breeding males or other non-breeding males. They may form somewhat stable alliances with other non-breeding males. The domestic and feral horses, Przewalski horses, and common zebra are known as harem breeders. Breeding typically occurs within stable single-stallion harem groups. Most of the stallions that have no harem form associations known as bachelor bands (Berger, 1986, pp. 174–195). These bachelor bands vary in size from two to fifteen or more individuals, and are less stable over time than harem bands. The majority of bachelor band members are yearling stallions leaving their natal bands and young adult stallions that have not yet held a harem. Occasionally an older stallion that has been displaced from his harem will join a bachelor band.

Our laboratory's principal research interest in bachelor bands concerns the socio-physiological mechanisms underlying bachelor band phenomena. For example, it is not known what social, physical, hormonal or other factors are involved in the emergence of a harem stallion from the bachelor band. A conspicuous feature of interaction among bachelor stallions is agonistic behavior, including mock and serious fighting, threats, avoidance, appeasement, and submissive behavior. Agonistic behavior among bachelors may serve to hone skills and develop physical stamina necessary to obtain and maintain a harem. It may also play a role in establishing an order of readiness for bachelors to join available harems (Berger, 1986, pp. 174-195). Preliminary to the study of these factors, we prepared the ethogram reported here. Our aim was to develop an illustrated catalog of agonistic behaviors observed among horse bachelor band stallions, succinctly annotated with verbal description and reference to further published description. Our emphasis was on simplicity and consolidation of information that would be useful as a practical field or laboratory research guide. This guide would also be useful for horse managers, animal keepers, veterinarians, and others interested in inter-male behavior or concerned with housing, grouping, and management of equids.

# 2. Methods

# 2.1. Behavior inventory from the literature

Literature (English language) pertaining to domestic and feral horses as well as other captive or free-running equids was reviewed to generate an inventory of behavioral elements

and sequences displayed during bachelor band agonistic interactions. Our working definition of agonistic behavior followed that of McFarland (1987, p. 13), which includes aggression, threat, appeasement, and avoidance behavior that occurs during encounters between members of the same species. His definition extends beyond behavior 'in direct response to an opponent' to include scent marking, ritualized threat behavior, vocalization, and advertisement. Key references on horse behavior include Feist (1971), Tyler (1972), Waring (1983), and Berger (1986). Each entry in the inventory includes a description of the behavior, a list of other names for the behavior, and a list of equid species in which the behavior has been reported among males.

A preliminary draft of our ethogram was circulated to 65 equine behavior researchers for review. This draft included a line drawing, photograph, and descriptive text for each entry. Twenty-eight researchers provided critical reviews (see acknowledgments). Subsequently, the ethogram presented here was amended and compiled into table format. It includes: an English name for each behavior (generally the most commonly used English term in the modern literature, and not necessarily the first name used in the literature), a line drawing depiction of the behavior, a text description, examples of other terminology used, and the equid species in which we had found descriptions of similar behavior among bachelor stallions. Finally, for some behaviors, we included comments concerning function or clarifying certain aspects of the behavior. The references to literature were chosen as readily available sources of further information. We did not attempt to provide an exhaustive inventory of all citations nor did we attempt to find the earliest description of the behavior. Behaviors were listed in alphabetical order, rather than grouped by proposed meaning or temporal association. In addition to these catalog entries, representative photographs (principally from this study but also from previous and subsequent studies of simulated bachelor bands of ponies at the same site) were included to further illustrate the context.

# 2.2. Original animal observations

In order to obtain photographic and video documentation of each inventoried behavior to develop more detailed descriptions and to identify any additional behaviors not found in the literature, we conducted direct observation of a simulated bachelor band, the result of pasturing fifteen pony stallions together in the same semi-natural enclosure (approximately 9 acres of woods and open grass, with a fresh water stream). In such a pasture grouping, one stallion assumes the role of 'harem stallion', vigilantly guarding an area within the stallion pasture along the fence line facing nearby mare pastures. The remaining stallions interact as a bachelor band. The stallions ranged in age from 2 to 21 years and in weight from 150 to 300 kg. All were sexually experienced for in-hand breeding. The group was observed for approximately 50 daylight hours over a 4 week period in June and July. For each observation session, the stallions were moved to a 2 acre pasture adjacent to their home pasture. The vegetation and terrain of the smaller pasture enabled continuous view of the entire enclosure. Based on previous observations of this and similar all-stallion groups, we knew that such crowding of an established bachelor band outside its home pasture greatly increases the frequency and intensity of agonistic interactions. This reduced the amount of time necessary to catalog the various types of behavior. We used an ad lib method of observation, scanning the entire group until detection of the initiation of an agonistic encounter of interest. Observation then focused on that interaction for its duration, before again scanning the entire group. Each focal interaction was video taped for descriptive documentation and photographed for use in subsequent preparation of line drawings.

## 3. Results

Table 1 represents our resulting bachelor band ethogram. Forty-four interactive behaviors and three complex sequences of behavior (fecal pile display, posturing, and ritualized interactive sequence) were cataloged. In addition, vocalization associated with these behavioral elements and sequences was described. In addition, the sequential context of some of these behaviors is shown in Figure series 1–4 and Figs. 5–35.

Most of the behaviors cataloged had been found in the English literature reviewed. Two additional behaviors were the very common (apparently evasive) behavior we called balk and the less common (apparently submissive) behavior, rump presentation.

# 4. Discussion

Included in this ethogram are what we found to be the conspicuous agonistic interactive behaviors of bachelor band stallions, based on observations of our pony bachelor band and descriptions found in the literature. No doubt there are other specific behaviors, particularly less conspicuous behavioral elements of communication, that we have not detailed. Certainly there are innumerable variations and combinations of facial expressions and vocalizations that play a role in communication. Vocalizations and elimination-marking behaviors are prominent features of bachelor interaction that require further evaluation. Nonetheless, the behavior included in this catalog should be an adequate base for further comparative or experimental research.

In the English literature surveyed, we found remarkably little focus on bachelor stallions. Detailed descriptions of specific agonistic interactions among bachelor equids were rare and scattered throughout the literature. The distinction between bachelor—harem stallion interactions and bachelor—bachelor interactions was not usually clearly conveyed. Description of bachelor interactions was mostly limited to broad terms such as fighting, playing, grazing, or grooming.

In our pony bachelor band, agonistic encounters varied considerably in their type and intensity, from very quiet affiliative behavior to serious aggression. Aggressive interactions ranged from those that seemed playful to those that appeared to be serious fighting. This finding is consistent with the Waring descriptions (1986, pp. 178–186). The range of tone of encounters was remarkably broad even when encounters involved similar basic behavioral elements and the same participants. Particular pairs of stallions often repeated similar aggressive sequences over a period of an hour or two, with a typical diminution of intensity and duration, until the agonistic encounter consisted of only abbreviated threat gestures with soft grunts or squeals 'in passing'. As the series of agonistic encounters decreased in intensity, the pair typically grazed side-by-side (see Figure series 1–3). Similarly, there was a trend over the period of this study for the intensity of encounters to subside more quickly within each subsequent observation session. While our goals and methods for this project preclude quantitative evaluation, it seemed evident in our simulated bachelor band that the greatest frequency and intensity of aggressive interaction was among moderately

dominant individuals as opposed to the clearly dominant or clearly low-ranking submissive band members. This, together with the fact that the frequency and intensity of aggressive encounters generally subsided over time suggest that the aggressive encounters may play a role in sorting out a dominance hierarchy. Our continuing observation of pastured bachelor bands indicates that, even after long periods (several months) together, stallions continue to exhibit posturing, mock fighting, chasing, and all other behaviors described in this ethogram, although at a reduced rate and intensity than when first grouped or re-grouped (S.M. McDonnell, unpublished observations, 1991).

Several conditions of our simulated bachelor band varied considerably from those of wild or feral populations. First, our group was composed of all post-pubertal stallions. Naturally occurring bachelor bands typically include at least a few yearling colts (Berger, 1986, pp. 181-182; Waring, 1983, pp. 142-143). In ongoing studies in our laboratory in which simulated bachelor bands have included immature, sexually inexperienced members, we have seen a high frequency of submissive behavior of immature stallions toward mature stallions, and markedly less aggressive interactions of mature stallions with the younger stallions. Secondly, our pony stallions all had in-hand breeding experience. Naturally occurring bachelor bands only occasionally have sexually experienced stallions, either bachelors that have bred young mares on the fringe of a harem, or stallions that have had and lost a harem (Feist, 1971). Finally, we deliberately provoked agonistic encounters by moving stallions from their home pasture to an adjacent pasture less than one fourth the size. This resulted in more frequent and intense encounters than would occur in an established pasture group, or than would be expected under feral conditions. In this regard, our crowded conditions may better simulate periods of disruption within naturally occurring bachelor bands, such as the arrival of a new bachelor group member or the departure of an established member. While these differences no doubt would be critical to a quantitative ethogram, we feel they are less critical to the nominally descriptive goal of this project.

One reason we know so little about equid male interactive behavior is that it is customary to stable and pasture mature stallions separately. This is to avoid fighting, which can be especially injurious when animals are crowded or continuously grouped and re-grouped. We successfully keep research pony stallions together in pasture bands of three to 20 mature stallions in appropriately spacious fields (usually 0.3–0.5 acres per pony stallion) with multiple watering sites. These animals incur remarkably few and minor injuries, despite spectacular inter-male agonistic interaction, at least when first grouped or re-grouped. Our observations are consistent with studies of behavior of Przewalski horse stallions pastured together (Tilson et al., 1988).

This ethogram addresses only one aspect of equid behavior, and is completely descriptive rather than quantitative. Similar compilations describing other equid behaviors, for example, feeding, resting, eliminative, reproductive, maternal, and play behavior, are needed to complete a comprehensive equid ethogram. Many of the agonistic behaviors of bachelor stallions may be the same behaviors that occur in other age–sex classes. For example, many of the behavioral elements of mock-fighting appear similar to play-fighting among juvenile males or adult with juvenile males still in their natal bands (Berger, 1986, pp. 179–181, 189–195). Similarly, behaviors such as alert, approach, avoidance/retreat, balk, bite, bite-threat, chase, ears laid back, follow, head-threat, interference, kick, kick-threat, lunge, nip, pawing, push, rump presentation, snapping, and certain vocalizations occur in females and juveniles in a variety of interactions. Further analysis is required to determine how similar those behaviors are to those of bachelor band stallions.

Table 1
Agonistic ethogram of the equid bachelor band

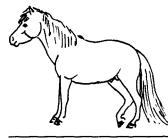
#### Alert

Rigid stance with the neck elevated and the head oriented toward the object or animal of focus. The ears are held stiffly upright and forward and the nostrils may be slightly dilated. (See Figs. 4(g), 5 and 6). The whinney vocalization may accompany this stance.

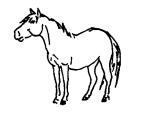
Other names: stand-stare (Feist, 1971, p. 91), stare (Waring, 1983, p. 182), standing alert (Duncan, 1985), vigilance (Berger, 1986, p. 44), attention face (zebra, Schilder and Boer, 1987) and, if the animal turns the body to face the object of interest, turn towards (asses, McCort, 1980, p. 100).

Comments: Alert posture may be followed by approach, followed by either friendly or aggressive interactions, or by resumption of the previous activity. Waring (1983, p. 176) described alarm as a stronger form of the alert stance, with eyes widely open and sclera showing. The behavior may include an arched neck and flared nostrils.

Species: horses (Feist, 1971, p. 36–39), Przewalski horses (S.M. McDonnell, unpublished observations, 1991), zebra (M.B.H. Schilder, personal communication, 1992), and feral asses (McCort, 1980, p. 100).



Approach



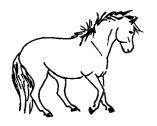
Forward movement toward another stallion in a straight or curving path. The approach can be at any gait or speed. The head may be elevated and ears forward or the head may be lowered and ears pinned back (see also herding and head threat). One stallion may approach another, or two stallions may simultaneously approach each other. Also, stallions may approach others to form larger assemblies. Approach may be followed immediately by retreat of a stallion being approached, or it may be followed by olfactory investigation, posturing, or fighting, which may evolve into a chase. (See Figs. 2(a) and 3(a).)

Other names: walk towards or run towards (McCort, 1980, p. 100).

Comments: Approach necessarily precedes most close agonistic interactions.

Species: horses (Waring, 1983, p. 176), Przewalski horses (Feh, 1988), zebra (Penzhorn, 1984; Schilder, 1988, 1990), and feral asses (McCort, 1980, p. 100).

## Arched neck threat



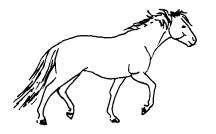
Neck tightly flexed with the muzzle drawn toward the chest. It is displayed concurrently with or as a component of many other behaviors, for example: posturing, parallel prance, pawing, olfactory investigation, strike threat. Arched neck threats are observed during close aggressive encounters and ritualized interactions. (See Figs. 2(c) and 4(c).)

Other names: arched neck (Berger, 1986, p. 44).

Comments: Arched neck threats are a component of most male-male interactions (Miller, 19891).

Species: horses (Miller, 1981; Berger, 1986, p. 133), has not been observed in zebras (M.B.H. Schilder, personal communication, 1991).

# Avoidance/retreat



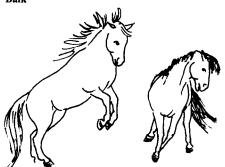
Movement that maintains or increases an individual's distance from an approaching stallion. The head is usually held low and ears turned back. The retreat can be at any gait but typically occurs at the trot. (See Fig. 7.)

Other names: facing away (Feist, 1971, p. 100), leaving (Schilder and Boer, 1987), avoidance behavior (Schilder, 1990), fleeing (Houpt and Wolski, 1980), passive reaction (Syme and Syme, 1979).

Comments: Waring (1983, p.177) used flight to refer to group retreat.

Species: horses (Miller, 1981), Przewalski horses (Waring, 1983, pp. 179–186), zebra (Schilder, 1990), and feral asses (McCort, 1980, p. 113).

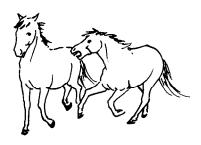




Abrupt halt or reversal of direction with movement of the head and neck in a rapid sweeping dorsolateral motion away from an apparent threat while the hind legs remain stationary. The forelegs may simultaneously lift off the ground. Typically associated with an approach or lunge of another stallion. (See Figs. 1(e-f), 2(g), 3(b), 4(f), 8, 29 and 31.)

Species: ponies, this study (no specific reference found to this behavior in other species).

Bite



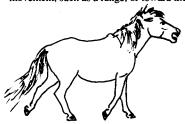
Opening and rapid closing of the jaws with the teeth grasping the flesh of another stallion. The ears are pinned and lips retracted. (See Fig. 8.)

Comments: Biting at each other's legs is common among bachelor stallions (Miller, 1981). Berger (1986, p. 134) found biting to be the primary fighting tactic of horses. Biting is also a conspicuous element of mare-stallion, stallion-mare, and mare-mare interactions.

Species: horses (Feist, 1971, p. 100), zebra (Penzhorn, 1984; Schilder, 1990) and Przewalski horses (Feh, 1988; Hogan et al., 1988; Keiper, 1988), feral asses (McCort, 1980, p. 100), and Asiatic wild asses (Bannikov, 1971).

#### Bite threat

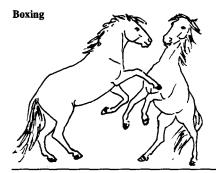
Similar to a bite except that no contact is made. The neck is stretched and ears pinned back as the head swings toward the target stallion. The miss appears deliberate, as opposed to accidental or successfully evaded by the target animal, thus giving the appearance of a warning to maintain distance. Bite threats are typically directed toward the other stallion's head, shoulder, chest or legs, and may be performed during an aggressive forward movement, such as a lunge, or toward the hind end of an animal being chased or herded. (See Fig. 9.)





Other names: bite-attempt (Berger, 1977), mouth open and attempt to bite (Feist, 1971, p. 39), bite (Syme and Syme, 1971).

Species: horses (Waring, 1983, pp. 179–182), Przewalski horses (Feh, 1988; Hogan et al., 1988), zebra (Schilder et al., 1984), feral asses (McCort, 1980, p. 113) and Asiatic wild asses (Bannikov, 1971).



Two stallions in close proximity simultaneously rearing and striking out with alternate forelegs toward one another. (See Figs. 10–11.)

Comments: Occurs usually amidst aggressive encounters and may precede dancing.

Species: horses (Waring, 1983, p. 180) and zebra (Penzhorn, 1984).

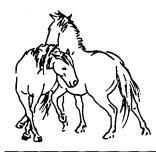
#### Chase

One stallion pursuing another, usually at a gallop in an apparent attempt to overtake, direct the movement of, or catch up with another stallion. The chaser typically pins the ears, exposes the teeth, and bites at the pursued stallion's rump and tail. The stallion being chased may kick out defensively with both rear legs. Chasing is usually a part of fight sequences. (See Fig. 3(e).)



Species: horses (Waring, 1983, p. 183; Feist, 1971, p. 100; Berger, 1986, p. 141), Przewalski horses (Hogan et al., 1988; Keiper, 1988), zebra (Schilder, 1988, 1990), and feral asses (McCort, 1980, p. 100).

#### Circling



Two stallions closely beside one another head-to-tail, pivot in circles, usually biting at each other's flanks, scrotum, rump and/or hind legs. With prolonged circling, the stallions may progress lower to the ground until they reach a kneeling position or sternal recumbency, where they typically continue to bite or nip one another. (See Figs. 1(n-s).)

Other names: head and neck wrestling (Houpt and Wolski, 1980, p. 41), leg drop (Berger, 1986, p. 45).

Species: horses (Feist, 1971, p. 102; Waring, 1983, p. 180), and zebra (M.B.H. Schilder, personal communication, 1991).

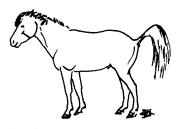
# **Dancing**



Two stallions rear, interlock the forelegs, and shuffle the hind legs, while biting or threatening to bite at one another's head and neck. (See Fig. 32.)

Species: horses (Waring, 1983, p. 181; Tembrock, 1968).

# Defecate over



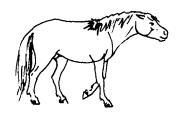
Defecation on fecal piles in a characteristic sequence: sniff feces, step forward, defecate, pivot or back up, and sniff feces again (see sniff feces and fecal pile display; Figs. 13 and 14).

Other names: elimination marking (Turner et al., 1981).

Comments: Stallions appear to compete to be last to defecate on a pile (McCort, 1984). Order within a group to defecate may be consistent with dominance hierarchy (Feist, 1971, p. 79).

Species: horses (Feist, 1971, pp. 89–102; Miller, 1981, p. 342), Przewalski horses (S.M. McDonnell, unpublished observations), zebra (Penzhorn, 1984; Schilder, 1988), and donkey (S.M. McDonnell, unpublished observations, 1991).

# Ears laid back/pinned



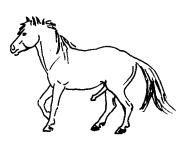
Ears pressed caudally against the head and neck. Typically associated with intense aggressive interaction. (See Figs. 8, 9, 18, 19, 28 and 34.)

Other names: ears retracted (Berger, 1986, pp. 44).

Comments: Waring (1983, p. 180) indicated that the ears are the most compressed at the most intense point of an aggressive interaction.

Species: horses (Feist, 1971, p. 39; Berger, 1986, p. 133; Waring, 1983, p. 178), Przewalski horses (Keiper, 1988), zebra (Schilder et al., 1984), feral asses (McCort, 1980, p. 105) and Asiatic wild asses (Bannikov, 1971).

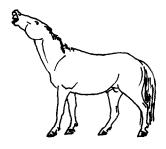
## **Erection**



Fully extended and tumescent penis. Observed during mild to moderately intense aggressive encounters. Bachelors will mount one another with an erection, and anal insertion has been observed (S.M. McDonnell, unpublished observation, 1991). (See Figs. 15 and 16.)

Species: horses (McDonnell, 1989), zebra (M.B.H. Schilder, personal communication, 1991), and fecal feral asses (McCort, 1980, p. 103.)

#### Flehmen

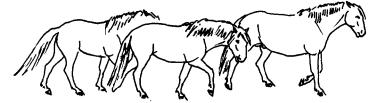


Head elevated and neck extended, with the eyes rolled back, the ears rotated to the side, and the upper lip everted exposing the upper incisors and adjacent gums. The head may roll to one side or from side to side. Typically occurs in association with olfactory investigation of feces.

Comments: Flehmen is believed to facilitate the drawing of fluids into the vomeronasal organ, enhancing the horse's olfactory capacity.

Species: all equids (Schneider, 1930; Stahlbaum and Houpt, 1989).

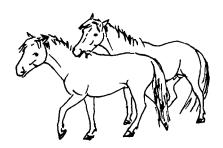
## Follow



Move along the path of another stallion, usually at the same gait as the stallion being followed. In contrast to a chase, there seems to be no attempt to direct the movement, attack, or overtake the leading stallion. (See Fig. 35.)

Species: horses (Waring, 1983, p. 173); Przewalski horses (Feh, 1988); and zebra (Schilder, 1990).

#### Grasp

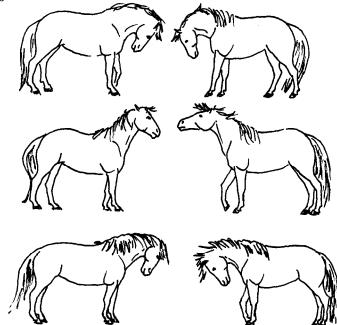


Similar to a bite, but a hold is maintained with the jaws and teeth, usually on the crest of the neck, or on a foreleg above the knee or hind leg above the hock.

Other names: biting the back of the neck (McCort, 1980, pp. 112-113).

Comments: Reportedly not common during intense fighting, but more common in play-fighting (Waring, 1983, pp. 179–180). Feral asses will grasp opponents and hold them as long as possible, sometimes rearing while holding onto an ear (McCort, 1980, p. 111). Species: horses (Berger, 1986, p. 73), zebra (M.B.H Schilder, personal communication, 1991) and feral asses (McCort, 1980, p. 113).

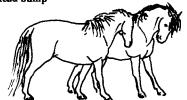
# Head bowing



Head bowing is a repeated, exaggerated, rhythmic flexing of the neck such that the muzzle is brought toward the point of the breast. Head bowing usually occurs synchronously betwen two stallions when they first approach each other head to head.

Species: ponies, this study; zebra (M.B.H. Schilder, personal communication, 1991).

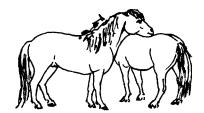
# Head bump



A rapid lateral toss of the head that forcefully contacts the head and neck of another stallion. Usually the eyes remain closed and the ears forward.

Other names: head swing (Feist, 1971, p. 99). Species: horses (Feist, 1971, p. 99; Syme and Syme, 1979).

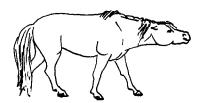
#### Head on neck, back, or rump



The chin or entire head rests on the dorsal surface of the neck, body, or rump of another stallion. Often precedes a mount. (See Figs. 1(u), 2(h), 4(g) and 17.)

Species: horses (Feist, 1971, p. 97), zebra (Schilder, 1988), and feral and asses (McCort, 1980, p. 106).

#### Head threat

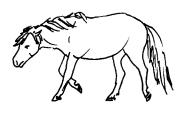


Head lowered with the ears pinned, neck stretched or extended toward the target stallion and, often, the lips pursed.

Other names: head extension (Waring, 1983, pp. 177–180), head swing (Feist, 1971, p. 102) when gesturing of the head and neck, head toss (Berger, 1986, p. 132). Species: horses (Waring, 1983, pp. 177–180); Wells and Von Goldschmidt-Rothschild, 1979), Przewalski horses (Feh, 1988), zebra (Penzhorn, 1984), and Asiatic wild asses (Bannikov, 1971).

# Herding





Combination of head threat and ears laid back with forward locomotion, apparently directing the movement of another stallion(s). (See Fig. 18.)

Other names: herding posture (Berger, 1986, p. 144), herding threat (Schilder et al., 1984), pointing (Schilder et al., 1984), driving (Wells and Von Goldschmidt-Rothschild, 1979). If the stallion's neck simultaneously oscillates from side to side, the behavior is termed snaking (Waring, 1983, p. 180).

Comments: Feist (1971, pp. 75-78) reported that herding is a behavior that is performed only by stallions. Although it is most common to see males herding females, male-male herding does occur.

Species: horses (Feist, 1971, p. 75; Miller, 1981; Waring, 1983, p. 180), Przewalski horses (Keiper, 1988) and zebra (Penzhorn, 1984).

#### Interference



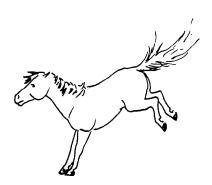
Disruption of combat of stallions by moving between the fighting individuals, pushing, attacking, or simple approaching the combatants. One or more stallions may simultaneously interfere with an encounter. (See Fig. 19.)

Other names: interposing (Schilder, 1990), intervene (Bannikov, 1971), lateral presentation (Penzhorn, 1984).

Comments: Bannikov (1971) reported that one or more wild ass stallions will intervene to protect a weaker individual from a stronger attacker.

Species: horses, Przewalski horses (Keiper, 1988), zebra (Schilder, 1990), and Asiatic wild asses (Bannikov, 1971).

## Kick

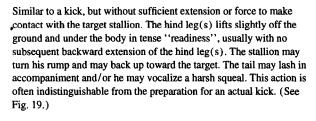


One or both hind legs lift off the ground and rapidly extend backwards toward another stallion, with apparent intent to make contact (in contrast to the kick threat described below). The forelegs support the weight of the body and the neck is often lowered. It is common for two stallions to simultaneously kick at each other's hindquarters, often associated with pushing each other's hindquarters. (See Figs. 1(v) and 20.)

Other names: hind-leg kick (Miller, 1981), rear-leg kick (Berger, 1986, p. 44), back kick (Keiper, 1988), and lift kick (McCort, 1980, pp. 103–107).

Species: horses (Berger, 1986, p. 44), Przewalski horses (Feh, 1988; Hogan et al., 1988), zebra (Schilder, 1990), and feral (McCort, 1980, pp. 103–107, 113) and Asiatic wild asses (Bannikov, 1971).

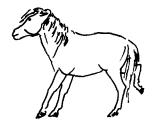
# Kick threat



Other names: rear threat (Wells and Von Goldschmidt-Rothschild, 1979), rear-leg lift (Berger, 1986, p. 44), threat to kick (Hogan et al., 1988), threat kick (McCort, 1980, p. 108).

Comments: As the term threat kick implies, this action seems to serve as a warning and as such helps to maintain distance between stallions. Keiper (1988) reported that, within Przewalski horse groups, the kick threat is second only to herding in frequency of aggressive actions exhibited.

Species: horses (Berger, 1986, p. 44; Waring, 1983, p. 180), Przewalski horses (Feh, 1988; Keiper, 1988; Hogan et al., 1988), zebra (Penzhorn, 1984; Schilder, 1990), and feral (McCort, 1980, p. 110) and Asiatic wild asses (Bannikov, 1971).



## Kneeling



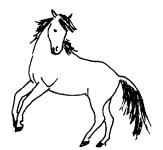
Drop to one or both knees, by one or both stallions engaged in face-to-face combat or circling with mutual biting or nipping repeatedly at the knees (fronts and backs of knees), head, and shoulders. (See Fig. 1(i).)

Other names: leg drop (Berger, 1986, pp. 134–135).

Comments: Berger (1986, pp. 134–135) proposed that the initial drop to the knees is an attempt to protect the forelegs from bites of the opponent. As such, this behavior may be a very important defensive action of equids.

Species: horses (Berger, 1986, pp. 73, 134–135), zebra (M.B.H. Schilder, personal communication, 1991), and Asiatic wild asses (Bannikov, 1971).

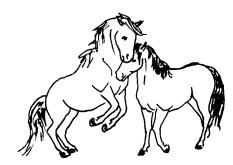
#### Levade



Similar to rear in that the front legs are lifted off the ground; however, the hind legs are placed well forward under the body, the hocks are deeply flexed, and the forebody does not rise as far off the ground. (See Figs. 1(g) and 21.)

Species: horses (Waring, 1983, pp. 34–35), zebra (M.B.H. Schilder, personal communication, 1992).

#### Lunge

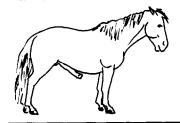


A swift forward thrust or charge from close range toward another stallion (usually toward his forebody), most often displayed concurrently with a bite threat, with ears pinned. (See Fig. 2(f).)

Other names: attacking (Schilder, 1988).

Species: horses (ponies, this study), Przewalski horses (S.M. McDonnell, unpublished observations, 1987), and zebra (Penzhorn, 1984; Schilder, 1988).

## Masturbation

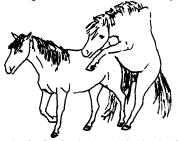


Erection with rhythmic drawing of the penis against the abdomen, with or without pelvic thrusting. Solitary or group activity. (See Fig. 22.)

Species: horses (Feist, 1971, p. 112), Przewalski horses (Boyd, 1991) zebra (Penzhorn, 1984), donkey (Henry et al., 1991).

#### Mount

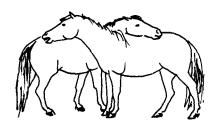
One stallion raises his chest and forelegs onto the other's back with the forelegs on either side, just as during copulation. Also seen are prolonged partial mounts, typically with lateral rather than rear orientation, and often with just one foreleg across the body of the mounted stallion (see Figs. 3(f,g) and 35). In a behavior similar to the initial mount orientation movements, termed head on neck, back or rump, the forelegs will not actually rise off the ground. These two behaviors may occur sequentially or independently of one another.



Comments: Schilder and Boer (1987) reported mounting and head-on-hindquarters as common in the plains zebra and suggested that this may play a role in establishing or confirming dominance hierarchies, since they typically supervene fighting episodes. However, others have suggested that mounting represents play behavior.

Species: horses (Berger, 1986, p. 183; Feist, 1971, p. 112), zebra (Schilder, 1988) and donkeys (S.M. McDonnell, unpublished observations, 1991).

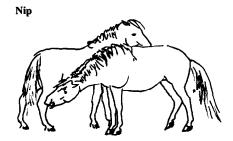
## Mutual grooming



Two stallions standing beside one another, usually head-toshoulder or head-to-tail, grooming each other's neck, mane, rump, or tail by gentle nipping, nuzzling, or rubbing.

Comments: In Przewalski horses, mutual grooming is reportedly more common among younger bachelors (Hoffmann, 1985).

Species: horses (Feist, 1971, pp. 46-49; Wells and Von Goldschmidt-Rothschild, 1988); Przewalski horses (Hoffman, 1985; Hogan et al., 1988), and zebra (Penzhorn, 1984; Schilder, 1990).

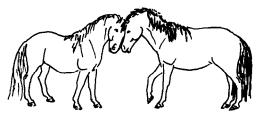


Similar to a bite, but with the mouth less widely opened and the teeth closing on only a small piece of flesh. Nipping is seen during play-fighting, during mutual grooming, and during moderate to serious aggressive interactions (J.C. Schulz, unpublished observations, 1991). (See Figs. 1(1) and 10.)

Species: horses (Houpt and Wolski, 1980, p. 43), Przewalski horses (Hoffmann, 1985), and donkeys (S.M. McDonnell, unpublished observations, 1988).

#### Olfactory investigation

Olfactory investigation involves sniffing various parts of another stallion's head and/or body. This behavior typically begins after stallions have approached one another nose to nose. After mutually sniffing face to face, typically one stallion works his way caudally along the other's body length, sniffing any or all of the following: neck, withers, flank, genitals, and tail or perineal region. During the investigation, it is common for one or both stallions to squeal, snort, kick threat, strike threat, or bite threat. (See Figs. 3(a), 4(b) and 23.)

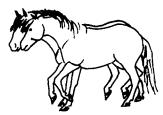


Other names: social investigation (Feh, 1988), genital inspection (Schilder, 1988), inspection (Schilder, 1990).

Comments: Genital sniffing is a prominent aspect of the investigation.

Species: horses (McCort, 1984), Przewalski horses (Feh, 1988), zebra (Schilder, 1990), and feral asses (McCort, 1980, pp. 103, 106–107).

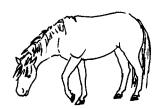
## Parallel prance



Two stallions, moving forward beside one another, shoulder-toshoulder with arched necks and heads held high and ears forward, typically in a high-stepping, slow-cadenced trot (passage, in dressage terminology). Rhythmic snorts may accompany each stride. Parallel prancing often immediately precedes aggressive encounters. Solitary prancing also occurs.

Species: horses (Feist, 1971, p. 91, 100; Berger, 1977; Waring, 1983, p. 183).

#### **Pawing**



One front leg is lifted from the ground slightly, then extended quickly in a forward direction, followed by movement backward dragging the toe against the ground in a digging motion. Most commonly, this action is repeated several times in succession. The stallion's nose may be oriented toward the substrate at which he is pawing or, if the activity is exhibited as a direct apparent threat to another stallion, the head will remain elevated and the neck arched. Pawing is frequently seen in aggressive encounters. It is also seen near fecal piles or dusty rolling sites, either as a solitary activity or during pair or group interactive encounters. (See Fig. 24.)

Comments: Houpt and Wolski (1980) suggested that pawing is a sign of frustration rather than aggression.

Species: horses (Feist, 1971, p. 91; Odberg, 1973; Waring, 1983; p. 183), Przewalski horses (Hoffmann, 1985), and donkeys (S.M. McDonnell, unpublished observations, 1991).

#### Push

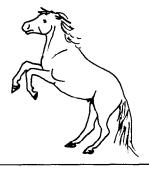


Pressing of the head, neck, shoulder, chest, body or rump against another in an apparent attempt to displace or pin the target stallion against an object. (See Figs. 1(i), 26, 27 and 28.)

Other names: bumping (Waring, 1983, p. 183).

Species: horses (Feist, 1971, p. 97; Waring, 1983, pp. 182–183), and zebra (Schilder, 1988).

## Rear



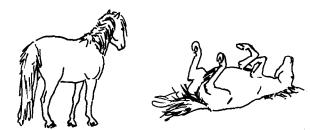
The forequarters are raised high into the air while the hind legs remain on the ground, resulting in a near-vertical position (see also boxing, dancing). While vertical, two stallions will rear in close proximity and attempt to bite one another on the head and neck or strike with the forelegs. (See Figs. 1(d,e,j,k,w), 2(e,g), 3(d), 10, 11, 29, 31 and 34.)

Comments: Rearing of one or both stallions during sparring often appears to be a means of demonstrating superior height.

Species: horses (Berger, 1986, p. 135), Przewalski horses (S.M. McDonnell, unpublished observations, 1991), zebra (Penzhorn, 1984), and feral asses (McCort, 1980, pp. 114–115).

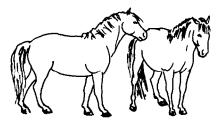
#### Rolling

Dropping from standing to sternal recumbency, then rotating one or more times from sternal to dorsal recumbency, tucking the legs against the body. Rolling typically occurs on dusty or sandy areas. Rolling is usually preceded by pawing and nosing of the ground and followed by body shaking. Snort vocalizations may occur when the stallion is nosing the ground or shaking.



Species: horses (Waring, 1983, pp. 39–40), Przewalski horses (S.M. McDonnell, unpublished observations, 1991), zebra (M.B.H. Schilder, personal communication, 1991) and donkeys (S.M. McDonnell, unpublished observations, 1991).

#### Rump presentation



One stallion positions its rump squarely in front of another stallion's head, lifting the tail slightly, reminiscent of estrous presentation of mares. The stallion to which the rump is presented usually sniffs the perineal region, and may push his shoulder against the hindquarters, and/or rest his chin or head on the rump, and may mount.

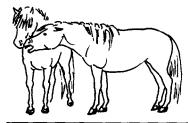
Comments: Rump presentation was exhibited by younger, lower ranking stallions to a clearly dominant stallion.

Species: ponies, this study.

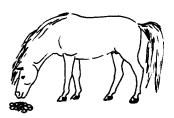
#### Snapping

Moving the lower jaw up and down in a chewing motion, usually with the mouth open and lips drawn back exposing the incisors. A sucking sound may be made as the tongue is drawn against the roof of the mouth (Waring, 1983, pp. 184–186). Typically, the head and neck are extended, with the ears relaxed and oriented back or laterally. It is usually performed while approaching the head of another, usually on an angle.

Other names: champing (Wolski et al., 1980), teeth-clapping (Feist, 1971, pp. 43-45), tooth-clapping (Boyd, 1980; Feh. 1988), bared-teeth face (Schilder and Boer, 1987), Unterlegenheitsgebarde (Zeeb, 1959), jaw-waving (Blakeslee, 1974) and jawing (McCort, 1980, pp. 100, 111). Comments: The name snapping was first used by Tyler (1972). It is commonly viewed as a submissive behavior, as it is mostly observed when a submissive or young stallion approaches an older or more dominant stallion and because a similar behavior has been noted in foals when approaching adults. Boyd (1980) concluded that snapping does not inhibit aggression by others but instead may serve to calm the submissive individual. Crowell-Davis (Crowell-Davis et al., 1985) suggested that snapping may be a "Displacement activity developed from nursing". A similar behavior, commonly called jawing, occurs at estrus in asses. Species: horses (Feist, 1971, pp. 43-45; Wells and Von Goldschmidt-Rothschild, 1979, pp. 365-372), Przewalski horses (Feh, 1988; Hogan et al., 1988), zebra (Schilder et al., 1984), feral asses (McCort, 1980, pp. 100, 113), and donkeys (S.M. McDonnell, unpublished data, 1991).



#### Sniff feces



Approach and sniff a previously voided feces or a fecal pile, usually as a part of a fecal pile display. This is almost always followed by defecating over the feces and again sniffing the pile. (See Figs. 1(b), 4(a) and 30.)

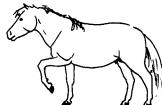
Other names: elimination marking (Turner et al., 1981).

Comments: It has been suggested (Ewer, 1968) that sniffing a fecal pile provides information regarding the hierarchical positions of contributing stallions.

Species: horses (Salter and Hudson, 1982), and Przewalski horses (Hoffmann, 1985).





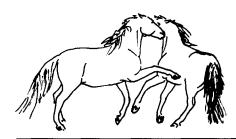


One foreleg is raised and lowered, sharply and firmly striking the ground, usually repeatedly. Stomping differs from pawing in that it is a vertical rather than horizontal movement of the leg. Stomping is most commonly seen during posturing and ritualized interactive sequences. (See Fig. 2(c).)

Other names: stamp (Waring, 1983, p. 183), front hoof beating (Hoffmann, 1985). Comments: Waring (1983, p. 214) reported that forceful contact with the ground emits an auditory signal.

Species: horses (Berger, 1977).

## Strike



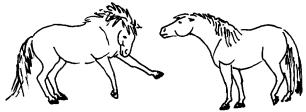
One or both forelegs are rapidly extended forward to contact another stallion, while the hind legs remain in place. The strike is typically associated with arched neck threat and posturing. A stallion may also strike when rearing. The strike is often accompanied by a squeal or snort. (See Fig. 31.)

Other names: front-leg kick (Berger, 1977, 1986, p. 44), paw-kick (Feist, 1971, p. 100).

Comments: The strike can also be observed during ritualized interactions, with the usual point of impact being the ground.

Species: horses (Waring, 1983, p. 183), Przewalski horses (Keiper, 1988), and Zebra (Klingel, 1967).

Strike threat



An abbreviated strike in which a foot is lifted off the ground in a gesture that mimics the preparation for an actual strike. However, no forward motion with the leg or contact with a target is actually made. The strike threat is often seen as part of ritualized interactions between stallions and is frequently accompanied by a loud squeal or snort. (See Fig. 4(b).)

Species: horses (Waring, 1983, p. 178), Przewalski horses (Keiper, 1988), and zebra (Klingel, 1967).

## Fecal pile display

A behavioral sequence occurring in association with defecation and fecal piles. Two or more stallions may participate, either simultaneously or in succession. These interactive sequences typically terminate with fighting, one stallion pushing the other away, or with calm separation as both stallions walk away from the pile.

- (1) approach fecal pile
- (2) sniff pile
- (3) flehmen
- (4) paw pile
- (5) step forward over pile or pivot around pile
- (6) defecate on top of pile
- (7) step backward or pivot over to sniff pile
- (8) may repeat all or part of sequence

Other names: elimination marking sequence (Turner et al., 1981).

Comments: There appears to be a communication or competition aspect in this activity. It has been suggested that the last to defecate is usually the dominant stallion (McCort, 1984). Miller (1981) reported that 25% of all agonistic stallion-stallion interactions took place at fecal piles.

Species: horses (Feist, 1971, pp. 56-58; McCort, 1984), Przewalski horses (Hoffmann, 1985; Boyd, 1988), zebra (Penzhorn, 1984), and feral asses (McCort, 1984).

## **Posturing**

Pre-fight head-bowing, prancing, stomping, olfactory investigation, as well as a stiffening of the entire body, including forelegs. The arched neck threat is also a major component, being held throughout most of the interaction. (See Fig. 25.) The participant may rub and push against one another.

Comments: Waring (1983, pp. 182–183) described the ears as forward and the tail elevated during much of the posturing.

Species: horses (Feist, 1971, p. 91; Berger, 1977; Waring, 1983, pp. 182–183).

#### Ritualized interactive sequence

Relatively consistently ordered agonistic sequence, described by Waring (1983, pp. 182–183):

- (1) stand stare (alert)
- (2) posturing (arched neck threat)
- (3) olfactory investigation
- (4) strike threats, pushing, squealing, and snorting
- (5) fecal pile displays
- (6) repetition of previous elements, often with increasing intensity

Species: horses (Waring, 1983, pp. 182-183; McCort, 1984).

# Vocalization (horses)

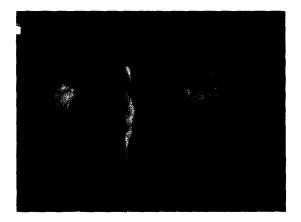
Whinney (neigh): loud, prolonged call, typically of 1-3 s duration, beginning high pitched and ending lower pitched. The head is elevated and the mouth slightly opened during the whinney. The whinney is associated with alert and approach from a distance, usually between an affiliated pair, and usually followed by a relatively friendly or playful interaction, as opposed to frank aggressive encounter.

Squeal: high pitched vocalization of variable loudness and typically of less than 1 s. The head can be in a variety of positions and the mouth is typically closed during the squeal. These vocalizations are typical during olfactory investigation, posturing, biting, nipping, as well as both mock and serious fighting.

Scream: of similar high pitch, but louder and longer than the squeal. Associated with the same situations as squeal, but typically with more serious aggression.

Snort: sound produced upon forceful quick exhalation of less than 1 s duration. Associated with olfactory investigation, prancing, posturing, and close combat involving rearing, boxing, kneeling and circling. Grunt: low-pitched vocalization of about 0.5 s duration. The mouth is closed during the grunt. As with the snort, the grunt is associated with olfactory investigation, posturing, and close combat involving rearing, boxing, kneeling and circling.

Other sounds: acoustical expressions, including hoof beats and other sounds produced by tail swishing, coughing, snapping, grazing, and snoring (Waring, 1983, pp. 198–215).





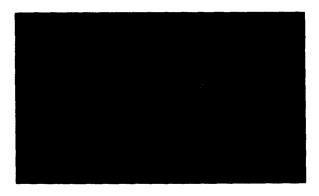


Fig. 1.







Fig. 1 (continued).





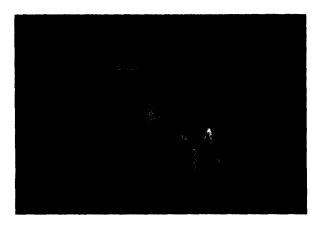


Fig. 1 (continued).











Fig. 1 (continued).

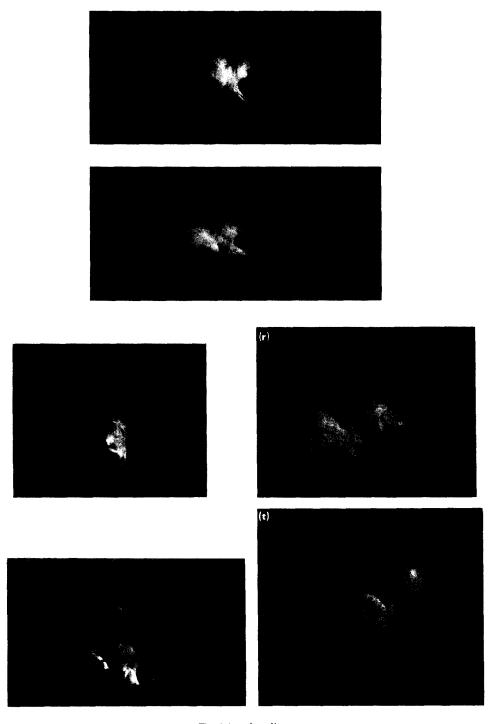


Fig. 1 (continued).





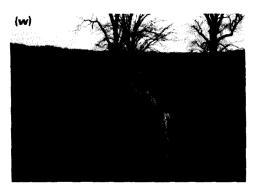


Figure series 1. Mock fight sequence of a pair that eventually formed a stable affiliation. (a) Nose-to-nose approach near fecal pile; (b) mutual sniff feces; (c) rolling near fecal pile (the pair alternated rolling and standing by); (d-f) rearing alternately; (g) levade (left) and balk (right); (h) mutual posturing and strike threats (accompanied by short, high pitched squeals); (i) push; (j-k) mutual rearing with boxing; (l) nipping hock; (m) head and neck wrestling; (n-s) circling, from standing position to kneeling, then sternal; (t) rising from sternal position; (u) head on body; (v) kick; (w) resumption of the sequence (j-v), which was completely repeated once and partially completed twice.



Fig. 2.



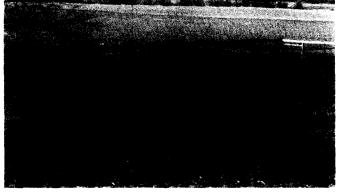




Fig. 2 (continued).







Fig. 2 (continued).

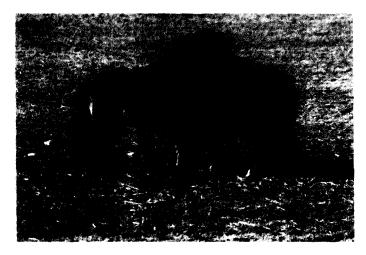


Figure series 2. Sparring encounter: (a) nose-to-nose approach and mutual sniffing; (b) nose-to-nose sniffing; (c) stomp; (d) strike threat; (e) simultaneous rear; (f) lunge; (g) rear (left) and balk (right); (h) head on body.

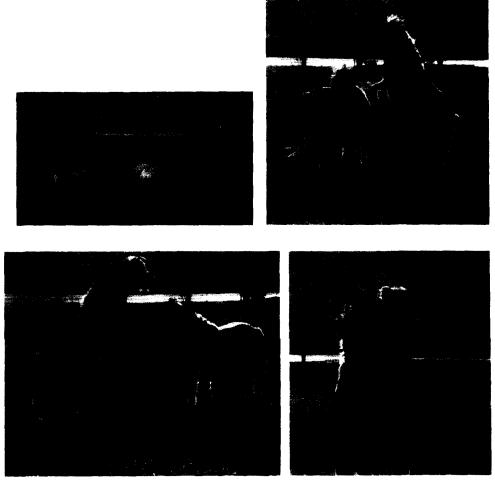


Fig. 3.





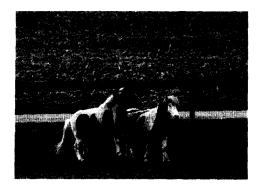


Figure series 3. Sparring, chase and mount: (a) nose-to-nose approach and mutual sniffing; (b-c) pair alternate rearing, notice balk (b, left); (d) mutual rearing; (e) chase; (f) mount; (g) leg on back (occurred during dismount, but position was noticeably prolonged).



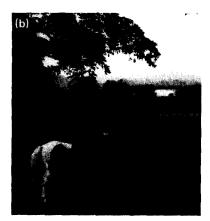


Fig. 4.

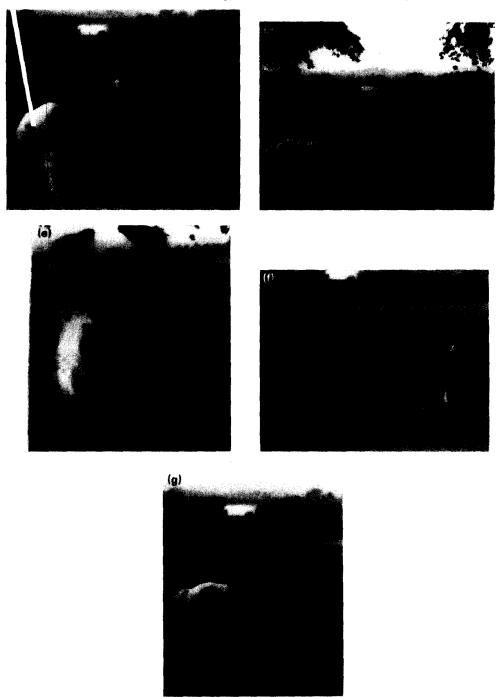


Figure series 4. Fecal pile display: (a) pair sniffing feces; (b) posturing with strike threat (right); (c) continued posturing with arched neck threat (right); (d) one stallion rears; (e) pair rears; (f) balk (right); (g) head on body, both alert to another pair encounter nearby.



Fig. 5. Alert.



Fig. 6. Three stallions simultaneously alert to nearby encounter.



Fig. 7. Retreat.



Fig. 8. Bite while lunging (right) and balk (left).



Fig. 9. Bite threat.



Fig. 10. Boxing.



Fig. 11. Boxing.

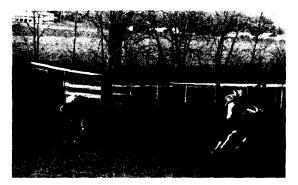
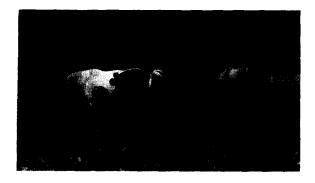


Fig. 12. Chase.



Figs. 13. Group elimination marking sequence.

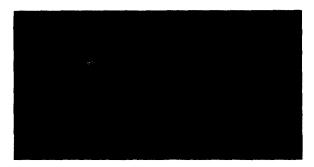


Fig. 14. Group elimination marking sequence.



Fig. 15. Erection.

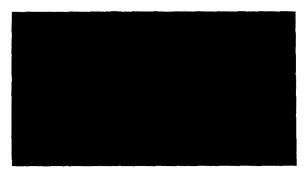


Fig. 16. Erection during mock fight.

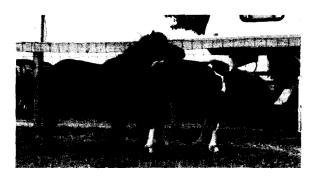


Fig. 17. Head on rump.



Fig. 18. Herding.



Fig. 19. Interference (dun stallion interrupting chase of paint stallion in background by bay stallion in foreground).



Fig. 20. Kick.



Fig. 21. Levade.

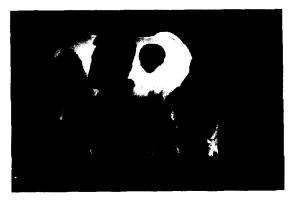


Fig. 22. Masturbation while grazing.



Fig. 23. Olfactory investigation sequence.



Fig. 24. Pawing feces, solitary.



Fig. 25. Posture.



Fig. 26. Push using head.



Fig. 27. Push using neck and shoulder.



Fig. 28. Tail-to-tail mutual pushing and kick threats.



Fig. 29. Rear (right) and balk (left).

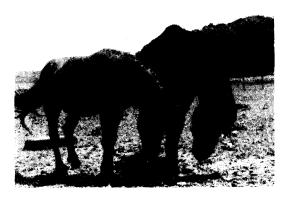


Fig. 30. Pair sniffing feces in synchrony.



Fig. 31. Strike (left), narrowly evaded by balk (right).



Fig. 32. Group encounter.



Fig. 33. Quiet grazing typically interspersed with aggressive activity.



Fig. 34. Two pairs sequentially engaging in fecal pile display (background pair) followed by mock-fighting near fecal pile (foreground pair, dancing with bite threat).



Fig. 35. Group encounter including mount and follow.

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# References

Bannikov, A.G., 1971. The Asiatic Wild Ass: neglected relative of the horse. Animalia, 13: 580-585.

Berger, J., 1977. Organizational systems and dominance in feral horses in the Grand Canyon. Behav. Ecol. Sociobiol., 2: 131-146.

Berger, J., 1986. Wild Horses of the Great Basin: Social Competition and Population Size. University of Chicago Press, Chicago, IL.

Blakeslee, J.K., 1974. Mother-young relationships and related behavior among free-ranging Appaloosa horses. Master's Thesis, Idaho State University, Moscow.

Boyd, L.E., 1980. The natality, foal survivorship, and mare-foal behavior of feral horses in Wyoming's Red Desert. Master's Thesis, University of Wyoming, Laramie.

Boyd, L.E., 1988. Time budgets of adult Przewalski horses: effects of sex, reproductive status, and enclosure. Appl. Anim. Behav. Sci., 21: 19-39.

- Boyd, L.E., 1991. The behavior of Przewalski's horses and its importance to their management. Appl. Anim. Behav. Sci., 29: 301-318.
- Crowell-Davis, S.L., Houpt, K.A. and Burnham, J.S., 1985. Snapping by foals of Equus caballus. Z. Tierpsychol., 69: 42–54.
- Duncan, P., 1985. Time-budgets of Camargue horses III. Environmental influences. Behaviour, 92(1-2): 188-208.
- Ewer, R.F., 1968. The Ethology of Mammals. Plenum Press, New York.
- Feh, C., 1988. Social behaviour and relationships of Przewalski horses in Dutch semi-reserves. Appl. Anim. Behav. Sci., 21: 71–87.
- Feist, J.D., 1971. Behavior of feral horses in the Pryor Mountain Wild Horse Range. Master's Thesis, University of Michigan.
- Grier, J.W., 1984. Biology of Animal Behavior. Times Mirror/Mosby, St. Louis.
- Henry, M., McDonnell, S. and Lodi, L.D., 1991. Pasture breeding behavior of donkeys under natural and synchronized estrus conditions. V International Equine Reproduction Symposium. J. Reprod. Fert. Suppl., 44: 77-86.
- Hoffmann, R., 1985. On the development of social behavior in immature males of a feral horse population (*Equus przewalskii* f. *caballus*). Z. Saugetierkd., 50: 302–314.
- Hogan, E.S., Houpt, K.A. and Sweeney, K., 1988. The effects of enclosure size on social interactions and daily activity patterns of the captive Asiatic wild horse Equus przewalski. Appl. Anim. Behav. Sci., 21: 147-168.
- Houpt, K.A. and Wolski, T.R., 1980. Domestic Animal Behavior for Veterinarians and Animal Scientists. Iowa State University Press, Ames.
- Keiper, R.R., 1988. Social interactions of the Przewalski Horse (Equus przewalskii Poliakov, 1881) herd at the Munich Zoo. Appl. Anim. Behav. Sci., 21: 89-97.
- Klingel, H. v., 1967. Soziale organisation und verhalten freilebender Steppenzebras. Z. Tierpsychol., 24: 580–624
- Klingel, H., 1975, Social organization and reproduction in equids. J. Reprod. Fertil. Suppl., 23: 7-11.
- McCort, W.D., 1980. The behavior and social organization of feral asses (*Equus asinus*) on Osabaw Island, Georgia. Ph.D. Thesis, Pennsylvania State University, State College.
- McCort, W.D., 1984. Behavior of feral horses and ponies. J. Anim. Sci., 58(2): 493-499.
- McFarland, D., 1987. The Oxford Companion to Animal Behaviour. Oxford University Press, 1987.
- Miller, R., 1981. Male aggression, dominance and breeding behavior in Red Desert feral horses. Z. Tierpsychol., 57: 340-351.
- Odberg, F.O., 1973. An interpretation of pawing by the horse. Saugetier Klundliche-Mitteilungen., 21: 1-12.
- Penzhorn, B.L., 1984. A long-term study of social organization and behaviour of Cape Mountain zebras (*Equus zebra zebra*). Z. Tierpsychol., 64: 97-146.
- Salter, R.E. and Hudson, R.J., 1982. Social organization of feral horses in western Canada. Appl. Anim. Ethol., 8: 207-223.
- Schilder, M.B.H., 1988. Dominance relationships between adult plains zebra stallions in semi-captivity. Behaviour, 104: 300–319.
- Schilder, M.B.H., 1990. Intervention in a herd of semi-captive plains zebra. Behaviour, 112: 53-83.
- Schilder, M.B.H. and Boer, P.L., 1987. Ethological investigations on a herd of Plains Zebra in a safari park: Time-budgets, reproduction and food competition. Appl. Anim. Behav. Sci., 18: 45-56.
- Schilder, M.B.H., van Hooff, J.A.R.A.M., van Geer-Plesman, C.J. and Wensing, J.B., 1984. A quantitative analysis of facial expression in the Plains Zebra. Z. Tierpsychol., 66: 11-32.
- Schneider, K.M., 1930. Das Flehmen. Zool. Gart., 3: 183-198.
- Stahlbaum, C.C. and Houpt, K.A., 1989. The role of the flehmen response in the behavioural repertoire of the stallion. Physiol. Behav., 45: 1207-1214.
- Syme, G.J. and Syme, L.A., 1979. Social Structure in Farm Animals. Elsevier, New York.
- Tembrock, G., 1968. Land mammals. In: T.A. Sebeok (Editor), Animal Communication: Techniques of Study and Results of Research. Indiana University Press, Bloomington, pp. 338-404.
- 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. Appl. Anim. Behav. Sci., 21: 169-185.
- Turner, J.W., Perkins, A. and Kirkpatrick, J.F., 1981. Elimination marking behavior in feral horses. Can. J. Zool., 59: 1561–1566.
- Tyler, S.J., 1972. The behavior and social organization of the New Forest ponies. Anim. Behav. Monogr. 5.

- Waring, G.H., 1983. Horse Behavior: The Behavioral Traits and Adaptations of Domestic and Wild Horses, Including Ponies. Noyes Publications, Park Ridge, NJ.
- Wells, S.M. and von Goldschmidt-Rothschild, B., 1979. Social behaviour and relationships in a herd of Camargue horses. Z. Tierpsychol., 49: 363–380.
- Wolski, T.R., Houpt, K.A. and Aronson, R., 1980. The role of the senses in mare-foal recognition. Appl. Anim. Ethol., 6: 121-138.
- Zeeb, K., 1959. Die 'unterlegenheitsgebarde' des n och nicht ausgewachsenen Pierdes (*Equus caballus*). Z. Tierpsychol., 16: 489-496.