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Stable design influences relaxation and affiliative behavior in horses during short isolation bouts

Emily J. Borthwick [a], Liane Preshaw [b], Charlotte Wheeler-Launder [b], Chloe Challinor [c], Nicola Housby-Skeggs [b], Esther Boalch [b], Sarah M. Brown [d,1], Gemma Pearson [a,b,*,1]

[a] *Royal (Dick) School of Veterinary Studies, Easter Bush, Roslin, United Kingdom*
[b] *The Horse Trust, Buckinghamshire, United Kingdom*
[c] *Hadlow College, Kent, United Kingdom*
[d] *The Roslin Institute and Royal (Dick) School of Veterinary Studies, Easter Bush, Roslin, United Kingdom*

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A B S T R A C T

Domesticated horses are often housed in individual stables for long periods where physical contact with conspecifics is not possible. Although common, this form of stable design is known to be detrimental to horse welfare. This study investigated the impact of short-term stabling (1-hour bouts) on behavioral expression using three stable conditions: a full wall, a barred window wall, and a half wall between paired horses in a within-subjects design study (N = 18). A mixed model (restricted maximum likelihood) was used to account for both stable condition and individual horse within the model. Behaviors influenced by stable design were those relating to vigilance and social affiliation. Horses spent a greater proportion of the observation time standing alert when in the full wall stable compared to the half wall stable ($P = 0.009$). The opposite is true of time spent standing and resting ($P < 0.001$). Compared to the window wall alone, horses in the half wall stable performed significantly more contact-seeking behaviors ($P = 0.021$). Horse owners often perceive stable design unimportant if only used for short periods of time, with the majority of their time budget spent at pasture with conspecifics. These results indicate that, even during short bouts of stabling, horses were more relaxed when stable design allowed them to engage in social behaviors with conspecifics and more vigilant when stable design left them physically isolated from conspecifics.

Introduction

The housing and management systems of domestic horses, *Equus caballus*, contribute toward their welfare. There are a variety of housing systems used to manage horses, the most popular being traditional housing which separates horses into individual stables (Waran, 2007). Other forms of equine housing allow increased visual and physical contact with neighboring horses, such as stabling with barred windows and housing horses together in small groups (Ninomiya et al., 2008). Although many horses are regularly stabled, this management system for horses has been identified as restricting the performance of affiliative behaviors, increasing stress, and as a potential risk factor for behavioral problems (Cooper et al., 2000; Hockenhull and Creighton, 2014; Lesimple et al., 2019).

Horses are highly social animals, spending the majority of their time in close proximity to conspecifics (Mills and Clarke, 2013; Beaver, 2019). Horses have been shown to work for social contact and have a high motivation to be in spatial proximity with conspecifics, highlighting the importance of and need for social interactions (Lee et al., 2011; Søndergaard et al., 2011). This creates a challenge to current housing systems where many horses are housed in individual stables with few opportunities for social contact.

Previous research has identified that long-term individual stabling increases the performance of stereotypies (Harewood and McGowan, 2005; Visser et al., 2008) and physiological response to stress (Yarnell et al., 2015). In contrast, providing horses with the choice to socialize with conspecifics when stabled has been shown to increase behaviors associated with positive affective states such as resting (Lesimple et al., 2019). This suggests that stable design has an impact on horse's behavioral responses, and housing horses in isolation from conspecifics has a negative effect on their welfare.

While existing literature has established the effects of prolonged stabling (12 hours per day [Yarnell et al., 2015], 8 hours per day

* Address for reprint requests and correspondence: Gemma Pearson, Royal (Dick) School of Veterinary Studies, Easter Bush, Roslin, EH25 9RG, United Kingdom.
E-mail address: gemma.pearson@ed.ac.uk (G. Pearson).
[1] These authors contributed equally.

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[Visser et al., 2008]) on the welfare of horses, there has been little research focus on short-term stabling bouts such as those that may be necessary for primarily field-kept horses prior to farrier or veterinary care. This may reflect a perception within the equestrian industry that short-term bouts of stabling would not affect welfare or represent a reluctance from scientists to investigate short-term bouts of stabling if they suspected they would be unlikely to demonstrate statistically different differences.

This study aimed to investigate whether there are differences in behavioral responses in adult domestic horses as a consequence of different stabling conditions during short stabling bouts (1 hour). It was hypothesized that increasing the opportunities for social contact during stabling will result in the performance of more affiliative behaviors and more behaviors indicative of relaxation.

Materials and Methods

Animals

A total of 18 equine residents of The Horse Trust, England, participated in this study. Horses were allocated to “closest companion” pairs based upon who spent the most time grazing and resting in close proximity to each other, as well as engaging in mutual grooming. Pairs remained consistent throughout the study. Each pair of horses was placed in adjoining stables during the 1-hour observation period and behaviors of both individuals were recorded.

Horses ages ranged from 11 to 28 years (mean = 22.31, SD = 4.31). There were 15 geldings and three mares with a range of breeds from the broad classification of UK native (n = 5), draft (n = 6), and warmblood/sports horse (n = 7) types. Horse’s backgrounds include rescue cases (n = 2) or retired working horses: military (n = 8), royal mews (n = 2), police (n = 2), and Riding for the Disabled Association (n = 4). All horses were familiar with being stabled and were only included on the basis that their carers did not consider that they found stabling stressful, that is, they did not show overt behaviors of acute stress such as vocalizing or not eating, among others. Aside from the two recue cases, all the others would have been stable for the majority of their working lives, with very limited turnout. Since moving to The Horse Trust, they were allowed to live out 24/7 in a socially stable herd. Horses would occasionally be kept as a group in large barns or stabled overnight individually if required for veterinary reasons. They were also familiar with being stabled for short durations while waiting for farrier care or to be petted by visiting members of the public. How frequently this occurred was highly variable.

Experimental design

The study involved a within-subject design, where each horse entered each stable condition once. The experiment was carried out during the months of May and June, 2021. To reduce order effect and treatment bias, a random generator function in Microsoft Excel 2013 was used to randomly allocate which treatment group horses were exposed to first. Horses entered each stable condition at similar times (between the hours of 11:14 and 14:29) to maintain consistency. Horses were exposed to only one condition per day.

Housing conditions

Three stable conditions—stabled alone full wall, stabled alone with a barred window in the wall, and stabled alone with a half wall (Table 1)—were used in this study. A total of six stables (commonly referred to as stalls or loose boxes in some parts of the world) were used; these were three groups of adjoining stables and were frequently used by resident horses. The location of stables on site at the stable yard is presented in Supplementary Figure S1.

Horses had hay and water provided ad libitum. Horses were exposed to each stable condition with their field companion in the adjoining stable. Outside of the observation periods, horses were at pasture. All horses except one had experienced the full wall stable condition before. Horses prior exposure to the window and half wall condition varied and were not known for each individual.

Behavioral observations

Continuous behavioral sampling was performed for 1 hour in each stable condition (total of 54 hours). An ethogram based upon previous research with similar study aims (Minero et al., 2015; Harewood and McGowan, 2005; Mal et al., 1991; Reid et al., 2017; Ruet et al., 2020; Yarnell et al., 2015) was used for behavioral analysis (Table 2).

Behavioral observations were collected using a total of three cameras per stable condition. These were a mixture of CCTV cameras (Dahua IPC-HDW5431R-ZE) and portable cameras (Canon HD LEGRIA HF R46 and Sony Handycam HDR-Cx625). Two of the cameras were placed inside the stables on opposite walls facing inside the stable and toward the door (Figure 1A-C) and one camera was placed outside the stables facing toward both stable doors (Figure 1D). Data collection of 1 hour began once handlers had placed each horse into the stable and the door had shut for the last horse that entered.

Reliability testing

A pilot study consisting of six horses in each stable condition (18 hours worth of data collection) was used to refine the ethogram and test intra-observer reliability. None of these horses were subsequently included in the main study. To reduce bias when carrying out data collection of behavioral measures, the order of watching videos and collecting data was randomly selected using the RAND function in Microsoft Excel 2013. The footage was analyzed using Observer XT software by one researcher, and six videos were watched twice. Duration behaviors (Table 2) were compared with percentage of agreement = 99%, kappa = 0.92. For the main study, the same researcher (EB) watched each video once; again, these were watched in a random order using the RAND function in Microsoft Excel 2013.

Table 1
Descriptions of the explanatory variables of three stable conditions that horses were exposed to in a randomized order in this study for 1-hour durations.

Stable condition	Description
Stabled alone full wall	A full wall separated each pair of horses. Horses could not be in physical contact with each other but had auditory and visual contact if both the horses had their heads over the stable door. The stable dimensions were 3.55 m × 3.44 m for each horse.
Stabled alone with window	A small barred window (1.21 m × 0.755 m) was in the wall of the adjoining stables. Horses had auditory and visual contact with their companion inside the stable; however, no physical contact was possible. The stable dimensions were 3.36 m × 3.58/3.53 m for each horse.
Stabled alone half wall	Horses had a half wall between adjoining stables measuring at 1.59 m in height. Horses were able to have physical, visual, and auditory contact with the horse in the adjoining stable. The dimensions of this stable were 4.67 m × 6.10 m for each horse.

Table 2
Ethogram of the behavioral indicators assessed for each horse in each stable condition.

Behavior	Definition	Source
Duration behaviors		
Stand alert	Horse is standing alert with eyes fully open, neck high, and tense with ears forward and body position showing alertness, looking intensely at environment.	Mal et al. (1991); Ruet et al. (2020); Yarnell et al. (2015); Visser et al. (2008)
Stand resting	One or both ears to the side, relaxed eyes, and neck (lower than when alert).	Lesimple et al. (2019); Visser et al. (2008)
Stand restless	Horse does not stand quietly but moves around in approximately the same spot and appears agitated.	Reid et al. (2017)
Stand dozing	Standing with head lowered, in posture typical of rest with eyes partially or fully closed and ears relaxed with resting hoof.	Harewood and McGowan (2005)
Locomote	Intentional movement of more than 2-3 steps.	Mal et al. (1991); Reid et al. (2017); Visser et al. (2008)
Feed	Horse is consuming hay or drinking water.	Mal et al. (1991); Yarnell et al. (2015)
Stereotypies	Weaving, crib biting, wind sucking, head shaking/nodding, box walking, and repetitive licking observed.	Yarnell et al. (2015)
Rest near	Horse is in close contact with other horse, close to touching and in close proximity of 1 m.	Minero et al. (2015)
Contact seeking	Horse is reaching and has their head positioned toward companion in the neighboring stable. Eye and ear positions suggest focus toward companion.	Reid et al. (2017)
Aggression	Horse is initiating or receiving aggression. Laid back ears, lowered head, and neck, dominant body position with threat to kick or bite.	Harewood and McGowan (2005); Ruet et al. (2020)
Lateral recumbency	Lateral thoracic area parallel to and in contact with the ground. Head immobile and legs extended with little or no movement.	Yarnell et al. (2015); Visser et al. (2008)
Other	Horse is engaged in behavior not included in any other category. For example, rolling	
Frequency behaviors		
Touch	Horses are touching nose-to-nose, sniffing, nuzzling, or resting head on another horse.	Minero et al. (2015)
Pawing	Horse lifting forelimb from ground slightly and extend forward quickly, drag toe backward against ground in digging motion repeatedly.	Harewood and McGowan (2005); Reid et al. (2017); Visser et al. (2008)
Head shaking	Rapid side-to-side rotation of head, neck, and upper body while standing with hooves planted.	Reid et al. (2017)
Kicking	Horse kicking at walls or door.	Reid et al. (2017)
Defecate/urination	Elimination of solid or fluid waste (feces or urine).	Reid et al. (2017); Visser et al. (2008)
Snorting	Horse has closed mouth, wide open nostril, and making a raspy noise.	Lesimple et al. (2019); Visser et al. (2008)
Vocalization	Neighing or whinnying with a loud, high-pitched sound.	Harewood and McGowan (2005); Reid et al. (2017); Visser et al. (2008)

Behaviors are classified by variable type (duration or frequency). Definition is given in column 2 with source cited in column 3.

Figure 1. Camera screenshot examples of stable conditions showing camera placement and angles per individual stable. (A) Full wall stable condition with camera mounted in the rear corner. A second camera was placed on the opposite wall in the adjacent stable, angled diagonally toward the window. (B) Window wall stable condition. A second camera was placed on the opposite wall to this camera, also angled diagonally toward the front window for full coverage. (C) Half wall stable condition. A second camera was placed on the opposite wall to this camera for full coverage. (D) Outside cameras placed in this position for each stable condition.

Statistical analysis

Results from the behavioral observations were extracted from Observer XT into Microsoft Excel 365 for data cleaning. The extraction provided a percentage of total observation time for duration behaviors and total count data for frequency behaviors. Behaviors of *lateral recumbency* and *aggression* were added into the behavioral observation of “*other*” due to recording little or no occurrence.

A general linear mixed model with a restricted maximum likelihood estimation method through a maximum of 100 iterations was carried out using Minitab® Statistical Software v.19 (Pennsylvania State University, USA). The Kenward-Roger approximation for fixed effects was applied (Kenward and Roger, 1997). Stable design (half wall, window wall, full wall) was included as a fixed effect with individual horse ID as a random effect. Variance component estimates generated by the model were used to assess the influence of individual differences between horses on the outcome measures. Due to a scheduling error, data for five pairs of horses were discarded in the window wall condition as these horses were exposed to two conditions in 1 day (with the window wall being the second condition); thus, a total of 18 horses (nine pairs) were used for both the full wall and half wall conditions, with eight horses (four pairs) also included in the window wall condition. The behaviors of *rest near* and *contact seeking* could only be accurately determined in the half wall and window wall conditions; therefore, the full wall was not included in the model for these behaviors. To preserve family-wise type I error assumptions, post hoc testing (Tukey honest significant difference test) was performed on behaviors that reached a significance level of 0.05 in the mixed effects model. *Touch* behavior was only possible in the half wall condition and is included as descriptive statistics only.

Ethical review

This research was granted ethical approval by the Veterinary Ethical Review Committee at the University of Edinburgh (April 23, 2021) with reference number 38.21.

Results

Full descriptive results for both duration and frequency behaviors are available in Supplementary Table S1.

Duration behaviors

Expression of the duration behavior “*stand alert*” was significantly different between stable conditions ($F_{(2,25.18)} = 5.8$, $P = 0.009$), with the highest expression of this behavior occurring in the full wall condition (mean = 18.77%, standard error of the mean [SEM] = 4.94, Figure 2). Tukey pairwise comparisons indicate a significant difference between the full wall and half wall conditions but not between the full wall and window wall or the window wall and half wall. Individual variability between horses accounted for 71.25% of total variance within the model ($Z = 2.505$, $P = 0.006$).

Expression of the duration behavior “*stand resting*” was significantly different between stable conditions ($F_{(2,24.96)} = 11.33$, $P < 0.001$), with the highest expression of this behavior occurring in the half wall condition (mean = 21.32%, SEM = 2.49, Figure 3). Tukey pairwise comparisons indicate no significant difference between the full wall and window wall conditions with both significantly different from the half wall. Individual variability between horses accounted for 52.36% of the total variance within the model ($Z = 2.007$, $P = 0.022$).

Object *licking* behavior was seen to differ between stable conditions ($F_{(2,27.89)} = 5.0$, $P = 0.014$) occurring predominantly in the half wall condition (half wall 5.84%: window wall 0.0%: full wall 0.012%). Licking occurred in the same spot on the wall of the stable in all observations, and so it was considered to represent an attractive stimulus, for example, increased salt availability in this part of the wall, rather than being stereotypical in nature.

The behaviors *stand restless, stand dozing, locomotion*, and *feeding* were not found to significantly differ between stable conditions (Table 3). Variance components analysis identified that individual differences between horses accounted for 81.18% of the observed differences in *feeding* behavior ($Z = 2.634$, $P = 0.004$) and 68.56% of the differences in *stand restless* behavior ($Z = 2.007$, $P = 0.006$), regardless of stable condition. The observed *box walking* behavior occurred in two horses with a contribution of 90.13% of the variance ($Z = 2.779$, $P = 0.003$) with no effect of stable condition on the behavioral expression. No other duration behaviors were observed to have statistically significant high individual variability (Supplementary Table S2).

The behaviors *rest near* and *contact seek* could only be reliably determined in the half wall and window wall conditions; thus, a restricted model was used. *Contact seeking* was found to differ between stable conditions ($F_{(1,6.49)} = 9.18$, $P = 0.021$) while *rest near* behavior did not (Table 3). *Contact seeking* occurred for longer

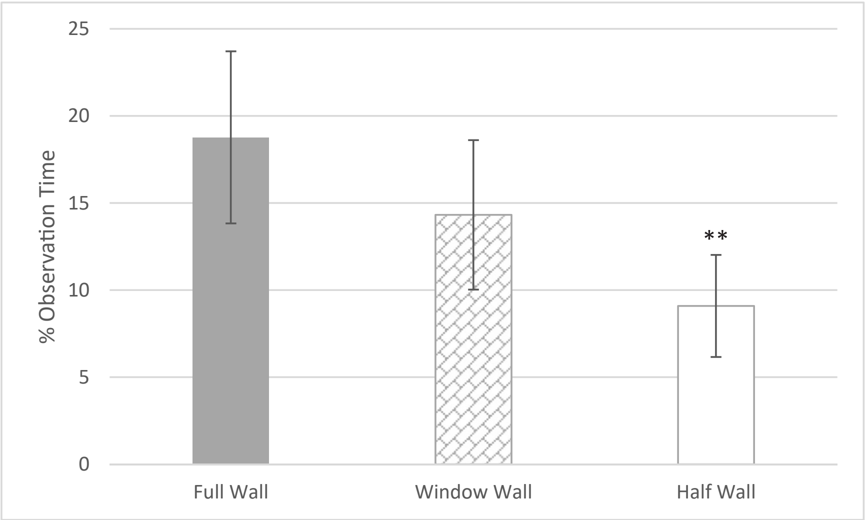

Figure 2. Mean percentage of total observation time in *stand alert* behavior by stable condition. Error bars are SEM. ** indicates a statistically significant difference between the full wall and half wall conditions ($P < 0.01$).

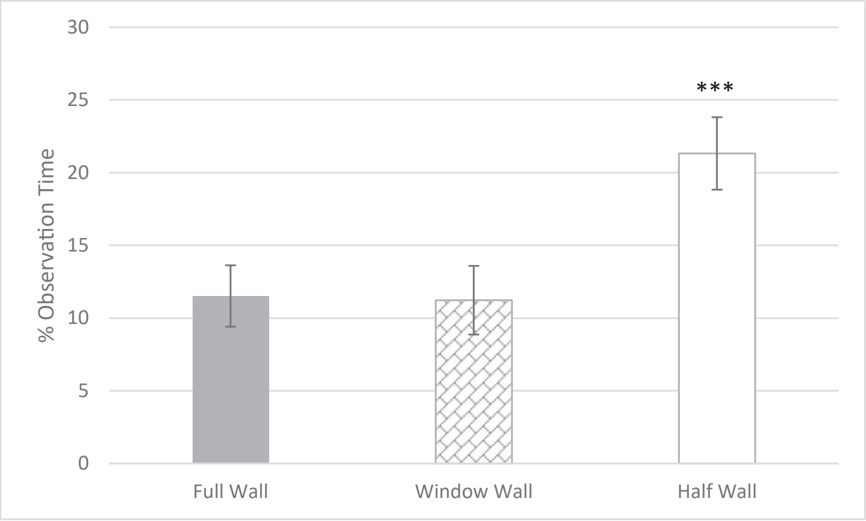

Figure 3. Mean percentage of total observation time in *stand resting* behavior by stable condition. Error bars are SEM. *** indicates a statistically significant difference between the half wall and both other conditions ($P < 0.001$).

Table 3
GLMM results showing the effects of stable conditions on duration behaviors observed.

Behavior	R-sq (%)	F statistic (stable condition)	*P* value
Stand alert	83.63	5.80	**0.009**
Stand resting	73.58	11.33	**< 0.001**
Stand restless	81.61	0.04	0.965
Stand dozing	86.79	0.13	0.878
Locomote	45.05	1.40	0.265
Feeding	88.43	3.38	0.051
Box walking	93.89	0.32	0.731
Object licking	20.48	5.00	**0.014**
Rest near	98.77	0.54	0.489
Contact seeking	94.08	9.18	**0.021**

R-sq value presented to represent model fit. Generalized Linear Mixed Model (GLMM), F statistic, and *P* value for effects of stable condition.
Significant values are indicated in bold.

periods in the half wall condition (mean = 0.58, SEM = 0.184) compared to the window wall condition (mean = 0.005, SEM = 0.028).

Frequency behaviors

None of the recorded frequency behaviors were different between stable conditions (Table 4) with the exception of "*touch*" which could only occur in the half wall and window wall conditions (mean = 1.22, SEM = 0.409). Eight out of 18 horses (45%) performed at least one touch behavior during the half wall stable condition, and this level of touch would not have been possible in the window wall condition.

Variance components analysis indicated that frequency behaviors showed high individual variability regardless of condition.

Table 4
GLMM results showing the effects of stable conditions on frequency behaviors observed.

Behavior	R-sq (%)	F statistic	*P* value
Pawing	73.67	1.04	0.370
Head shaking	38.84	0.34	0.715
Kicking	47.83	0.89	0.423
Defecate/urinate	80.99	0.50	0.615
Snorting	71.70	0.31	0.733
Vocalization	92.45	1.82	0.183

R-sq value presented to represent model fit. Generalized Linear Mixed Model (GLMM), F statistic, and *P* value for effects of stable condition.

Individual differences between horses occurred for ~60-80% of the observed variability in *vocalization, defecation, snort* and *paw* behaviors, and ~20-30% of the variation in *kick* and *head shaking* behavior (Supplementary Table S2).

Discussion

Duration behaviors

This study supports previous research which found increased *stand alert* behaviors when horses were housed in individual stables with no contact with conspecifics, similar to the full wall design (Visser et al., 2008; Lesimple et al., 2019). It has been suggested that this behavior indicates hypervigilance and stress, and hence, indicating an increased compromise of horse's welfare (Young et al., 2012). Horses rely on conspecifics for survival due to mutual vigilance, and when horses are in groups, there is a reduced risk of predation (Waran, 2007). Therefore, behaviors of *stand alert* may have occurred as horses could not see each other when inside the full wall stable, meaning communication of potential threats is reduced and horses would need to observe their environment more intensely. Similarly, the increase in behaviors of *stand resting* when in the half wall condition supports previous research (Lesimple et al., 2019) indicating that relaxation behaviors occur as social contact is increased. The presence of conspecifics is an important coping mechanism and can reduce the negative responses to stressful challenges (VanDierendonck and Spruijt, 2012). Therefore, behaviors of *stand resting* may have occurred more in the half wall stable due to horses being in contact with conspecifics, highlighting the importance of social contact as it can alleviate stress responses and increase positive behaviors of relaxation (Hebesberger, 2021).

In line with previous research (Yarnell et al., 2015), horses were shown to spend a small amount of time engaged in *contact seeking* behavior. Existing research has found social interactions to occur when horses are stabled long-term over consecutive days (Heleski et al., 2002; Visser et al., 2008; Yarnell et al., 2015); however, this study shows that, even in short-term stabling with known partners, horses will engage in social behaviors when given the opportunity. Previous studies have shown that the motivational strength for social contact in horses is high, with horses consistently performing operant tasks to gain access to social contact (Lee et al., 2011; Søndergaard et al., 2011), even when social isolation is not long term. Thus, it is probable that, even in normally group-living individuals, the importance of social support during stabling remains high. Although no significant differences in *rest near* behaviors and stable conditions were found, this behavior did occur when horses were in the window and half wall stable. Social bonds in horses are maintained via affiliative behaviors such as spatial proximity (Wolter et al., 2018). Therefore, not only does stabling horses in contact with conspecifics appear to increase relaxation, but it can also maintain social bonds among group members.

Aggression was observed very infrequently in this study; this may be due to the fact that horses were stabled next to the horse; they were observed to be in close proximity most frequently out at pasture and so already very tolerant of each other. Therefore, these responses may be different if housing unfamiliar horses (such as at a competition venue, although this is highly unlikely anyway as biosecurity is also an important consideration) or horses that do not get on well in close proximity to each other.

This study found two horses performed the locomotor stereotypical behavior of box walking that was not affected by stable design. Previous research in this field has suggested that locomotor stereotypies occur due to lack of social contact and restricted movement, resulting in barrier frustration (McGreevy et al., 1995; Cooper et al., 2000; Clegg et al., 2008; Visser et al., 2008; Sarrafchi and Blokhuis, 2013). However, it is known that stereotypies evolve once they have been established, and in mature animals, such behaviors can become more difficult to eradicate over time (Waters et al., 2002). Other research has also suggested that some stereotypies/abnormal repetitive behaviors act as a rewarding system in the brain, which results in the maintenance of such behaviors (Sarrafchi and Blokhuis, 2013). Differences in neurophysiology exist between oral and locomotor stereotypies (Hemmings et al., 2018), which may explain why it is possible to resolve locomotor stereotypies once established but not oral stereotypies. This behavior may have been well established in these two horses, and placing them in an environment that has high standards of welfare, such as a stable with increased social contact, could not prevent or reduce box walking behaviors without also implementing a behavior modification program.

Frequency behaviors

No frequency behaviors were found to be influenced by stable design with the exception of touch behavior, which was only possible and occurred in the half wall condition. This finding is consistent with Yarnell et al. (2015) who also found that, when horses are provided with the choice of touching conspecifics in neighboring stables, they will perform this behavior. The fact that these horses chose to perform this behavior in the 1 hour stabled when they can perform it ad libitum the other 23 hours a day demonstrates that it is highly valued. We suggest that performing touch behaviors became even more important in a restricted environment than it is at pasture, where they were using it for social support. A higher frequency of allogrooming has been demonstrated during stressful conditions in Quarter Horse mares, supporting the concept of a social coping mechanism in response to stress (Kieson et al., 2023). A similar increase in affiliative social behaviors has been reported in stallions stabled in groups (Christensen et al., 2002) and where horses, normally kept in individual boxes, were given temporary access to pasture (Christensen et al., 2002; Ruet et al., 2020). It is likely that providing a half wall stable, allowing for the expression of natural social behaviors, has a positive effect on the welfare state of stabled horses, even for very short durations. Previous research has found increased vocalizations in stables with high amounts of social isolation (Harewood and McGowan, 2005); however, this could not be confirmed here. We observed vocalization to be highly individually variable, with just two horses performing the majority of vocalizations throughout the study. These horses were also the two who performed box walking behaviors, suggesting that these individuals found stabling in general to be a more stressful experience than others.

Individual variability

Consistent with previous work (Pearson, 2022), there was individual variability in how horses responded to stabling in each condition. While it is tempting to think that some horses are able to cope with solid wall stables, it should be remembered that stress is expressed differently depending on their individual coping mechanism (Pearson, 2022). Ultimately, this study provides sufficient evidence to demonstrate that as a species horses are less stressed in housing that allows social contact.

Limitations

The sample size was based on previous research (Yarnell et al., 2015). However, this was not undertaken using a sample size calculator, which would have been preferable prior to commencing data collection. A further limitation of this study was the reduced number of horses for which data for the window wall condition were included (8 vs. 18). While it is possible that, with 18 horses in the window wall condition, the results for stand resting and stand vigilant may have been slightly different, we are confident this would not be the case, based on both evaluation of the excluded data and also when analyzing the data of only the eight horses included in all three conditions. Furthermore, the fact that the window wall results, even with smaller numbers, were significantly different from the half wall does suggest that physical contact is more important than visual contact and that a window wall is unlikely to be equivalent to a half wall design; this is in line with other work. Despite this, we also acknowledge that the financial costs of modifying a full wall to a half wall are considerably higher than modifying to include a window. As horses spent slightly less time stood alert in the window wall design, it is possible this design provides an intermediate level of welfare and provides justification for further study.

Conclusion

Horses displayed less vigilance, spent time relaxed, and performed affiliative social behaviors when housed in half wall stables. This demonstrates that, even in horses familiar with stabling and when only stabled for very short durations (1 hour), providing physical contact in stable design allows for improved welfare. This study directly challenges the notion that stable design is less important in horses only housed for brief periods of time and that are otherwise kept at pasture with conspecifics. This study contributes to existing knowledge regarding housing designs and their important effects on animal welfare, supporting the argument that friends, forage, and freedom are required for good horse welfare. In particular, this highlights the strong need for social contact in horses and a possible strategy for accommodating this in management and building design.

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Author contributions

The idea for the paper was conceived by LP and GP. The experiments were designed by GP, SMB, and EJB. The experiments were performed by EJB, CW, NHS, CC, and EB. The data were analyzed by

SMB. The paper was written by SMB, EJB, and GP. All authors approved the final version.

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Conflict of Interest

The authors have no conflict of interest to declare.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jveb.2023.10.003.

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