Current Zoology, 2025, **71**, 137–151
https://doi.org/10.1093/cz/zoae052
Advance access publication 16 September 2024
Original Article

Yawning in sync: implications for social cohesion in horses

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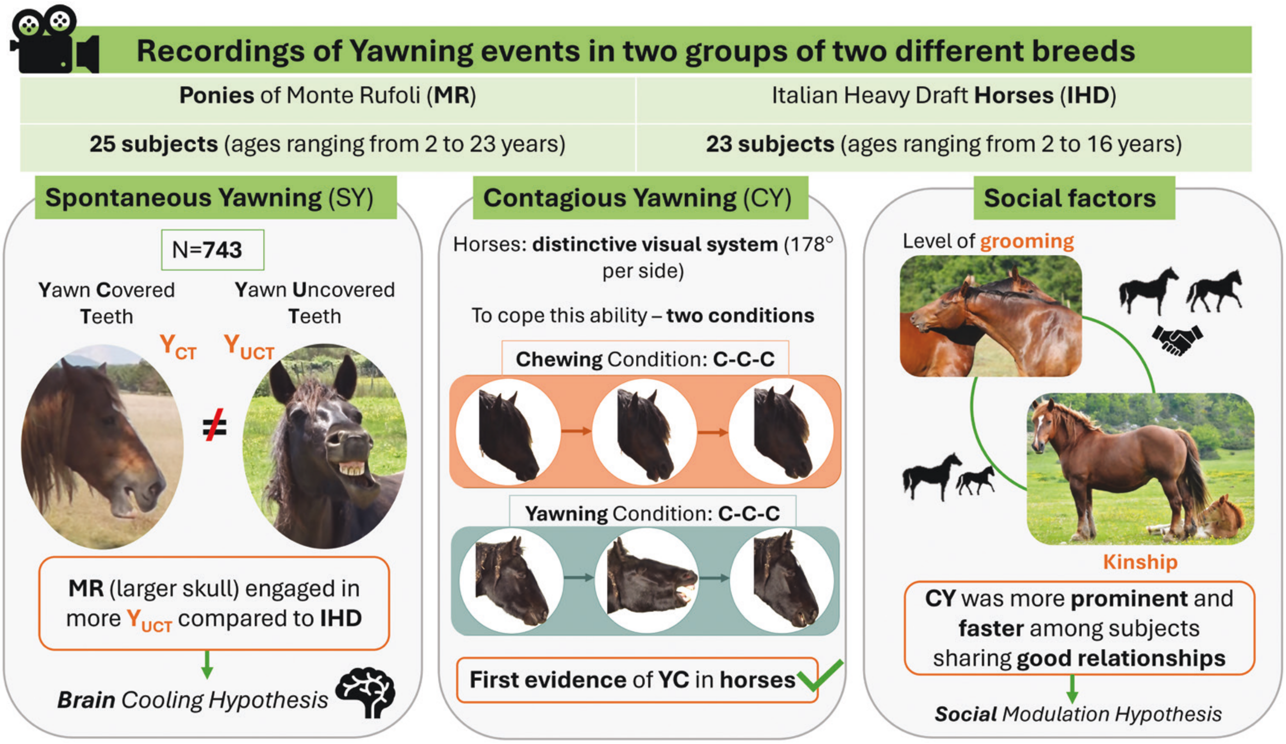
Handling editor: Zu-Shi Huang

Abstract

The increasing interest in the study of spontaneous (SY) and contagious yawning (CY) was so far focused on several taxa, especially primates. Here, we focused on SY and CY in horses, a suitable species due to their complex social dynamics that has been largely overlooked in research on these phenomena. By analyzing videos of 48 horses on pasture, we identified 2 yawning morphologies: Covered (Y_{CT}) and Uncovered Teeth (Y_{UCT}). Using EquiFACS, we quantitatively demonstrated that Y_{CT} and Y_{UCT} differ in terms of muscle recruitment. Moreover, we provide the first evidence for the presence of CY by comparing 2 different conditions: chewing-yawn-chewing versus chewing-chewing-chewing. Supporting the *Social Modulation hypothesis,* in our mares, CY was more prominent among subjects sharing good relationships. Moreover, subjects responded more rapidly to kin compared with non-kin and kin frequently grooming each other responded even more rapidly to each other yawns. The high familiar yawn sensitivity can provide selective advantages increasing behavioral synchronization and group cohesion.

Key words: EquiFACS, *Equus caballus*, social modulation hypothesis, Yawn contagion, yawn morphologies.

Graphical Abstract



Received 21 May 2024; accepted 10 September 2024

Yawning is present in all vertebrates, from the fetal stage to the adult age (Blanton 1917; Schiller 2002; Provine 2005; Matikainen and Elo 2008; Massen et al. 2021; Gallup 2022). It is considered a fixed action pattern being unstoppable, uncontrollable, and morphologically similar across species (Deputte 1994; Walusinski and Deputte 2004; Provine 2010). From a mechanistic perspective, yawning involves basically 3 different phases: 1) a slow and wide opening of the mouth, with a deep inhalation, 2) a quick closure of the mouth accompanied, and 3) by a brief exhalation (Barbizet 1958).

Although challenging to distinguish, the functions attributed to yawning can be categorized based on the distinct physiological conditions of the yawner (*Physiological domain*) and the social situations in which yawning occurs (*Social domain*) (Guggisberg et al. 2010). Obviously, all these hypotheses, both between and within domains, are not necessarily mutually exclusive, probably being the 2 faces of the same coin (e.g., proximate vs ultimate explanations). Yawning can be implicated in regulating physiological functions, including blood oxygen levels (Guggisberg et al. 2010), thermoregulation (Miller et al. 2010; Gallup and Eldakar 2013), brain cooling (Gallup and Eldakar 2013), states of drowsiness and arousal (Deputte 1994; Zilli et al. 2008; Guggisberg et al. 2010; Gallup 2022). The *Thermoregulation hypothesis* suggests that yawning helps reduce body and brain temperature, responding to environmental temperature changes (Massen et al. 2014; Eldakar et al. 2015; Massen and Gallup 2016). The *Drowsiness hypothesis* links yawning to changes in alertness during periods of inactivity, and it is largely explored in both humans (Greco et al. 1993; Provine 2005; Giganti et al. 2010; Gallup and Meyers, 2021) and in different non-human mammals (*Otaria flavescens*, Palagi et al. 2019; *Loxodonta africana*, Rossman et al. 2017; *Crocuta crocuta*, Casetta et al. 2022; *Pan troglodytes*, Vick and Paukner 2010; and *Theropithecus gelada,* Leone et al. 2014). The *Brain Cooling Hypothesis*, a form of thermoregulation, suggests that yawning dissipates heat by increasing blood flow, acting as a radiator (Gallup and Gallup 2008; Gallup et al. 2016, 2020; Massen et al. 2021). Lowering brain temperature improves mental performance and alertness. Yawning promotes cooling through inhaling cool air (Gallup and Gallup 2008; Gallup et al. 2016; Massen et al. 2021). Baenninger (1997) highlights that spontaneous yawning can be also influenced by social context. The *Social Distress hypothesis* (Altmann 1967; Deputte 1994) states that yawning as well as self-scratching, a self-directed behavior predicting anxiety in mammals (Palagi et al. 2019), rises after agonistic events, suggesting a connection of yawning to anxiety (*Melopsittacus undulatus*: Miller et al. 2010; *Rattus norvegicus:* Moyaho and Valencia 2002; *Otaria flavescens:* Palagi et al. 2019; *Lemur catta* and *Propithecus verreauxi*: Zannella et al. 2015; and *Theropithecus gelada*: Leone et al. 2014).

Although yawning has been extensively studied in primate and carnivore species, literature on ungulates is deficient (Baenninger 1997; Gallup 2011). Domestic horses (*Equus ferus caballus*) are a rare case where yawning has been described (Fureix et al. 2011). The authors found that horses exhibit more yawning and stereotypical behaviors (e.g., lip play, head shaking and nodding, weaving) in pre-feeding than during/after feeding, suggesting a possible linkage between yawning and anxiety also in horses. In Przewalski horses (*Equus ferus przewalskii*), a study revealed an association between yawning and aggressive behavior especially in bachelor males that frequently engage in agonistic encounters. Additionally, stallions yawned more than adult females and immature males (Górecka-Bruzda et al. 2016). The authors suggest that stallions' yawning can be triggered by higher testosterone levels and social stress deriving from male–male interactions.

Despite the fixed nature of yawning, data exist underlining the presence of a certain degree of variability (Walusinski and Deputte 2004; Guggisberg et al. 2010; Vick and Paukner 2010; Provine 2012; Leone et al. 2014; Gallup et al. 2016; Massen et al. 2021). In primates, larger yawns (also called "threat yawns," Altmann 1967) are expressed more by males than females and occur under high-tension situations (Leone et al. 2014). Moreover, especially in species with high sexual dimorphism, males exhibit larger yawns during territorial defence or competition for females (Zannella et al. 2015, 2017). In primate species, the diverse yawn morphologies, defined based on teeth visibility, are distributed differently as a function of the social context (*Pan troglodytes:* Vick and Paukner 2010; *Theropithecus gelada:* Palagi et al. 2009; *Macaca* sp.: Zannella et al. 2021).

Despite the widespread presence of spontaneous yawning across vertebrates (Heusner 1946; Baenninger 1997; Massen et al. 2021), contagious yawning (CY) (the response to others' yawns with a yawn) seems to be present in highly cohesive and social species (Guggisberg et al.2010). CY is described as a response to an innate releasing mechanism (Provine and Hamernik 1986; Bartholomew and Cirulli 2014) and it has been observed between individuals of the same species (e.g., ungulates: Yonezawa et al. 2017; Norscia et al. 2021; primates: Palagi et al. 2009; Demuru and Palagi 2012; van Berlo et al. 2020; carnivores: Romero et al.2014; Wojczulanis-Jakubas et al. 2019; Casetta et al. 2021, 2022; Ake and Kutsukake 2023; birds: Miller et al. 2012) or different species (proboscidates: Rossman et al. 2020; primates: Cambpell and de Waal 2014; Gallup and Wozny 2022; Pedruzzi et al. 2022; carnivores: Romero et al.2013). One study on horses (*Equus caballus*) provided no evidence for CY in this species (Malavasi 2014).

Although the issue is highly debated and far to be completely demonstrated (Massen et al. 2012; Massen and Gallup 2017; Neilands et al. 2020), different authors suggest that the phenomenon of CY could be influenced by social factors (*Social Modulation hypothesis)*: the better the relationship quality of the subjects, the higher their reciprocal susceptibility to CY and shorter response latency (Romero et al. 2014). Most of the data about the *Social Modulation hypothesis* come from primate species such as red-capped mangabeys (Pedruzzi et al. 2022), geladas (Palagi et al. 2009; Pedruzzi et al. 2022), chimpanzees (Campbell and de Waal 2011, 2014), bonobos (Demuru and Palagi 2012), and humans (Norscia and Palagi, 2011; Palagi et al. 2014).

Recent findings suggest that CY helps synchronize group activities. In lions (*Panthera leo*), yawning is a reliable indicator of the imminent behavioral state changes. CY between the 2 agents promotes their subsequent behavioral alignment (Casetta et al. 2021). Behavioural synchronization between group members is crucial to social life and plays a central role in maintaining inter-individual cohesion (Engel and Lamprecht 1997; Gautrais et al. 2007; King and Cowlishaw 2009). A study based on a social network involving more than 100 feral horses living in a multi-level society showed that subjects belonging to the same unit synchronize their activities (e.g., resting or moving) more than subjects belonging to different unit (Maeda et al. 2021). Synchronisation also contributes to increase efficiency in group vigilance (Pays et al. 2007; Beauchamp 2015) thus reducing predation risk, again especially in ungulates (*Equus caballus*: Souris et al. 2007; *Bos taurus*: Šárová et al. 2013).

Here we focus on spontaneous and CY in horses. As a first step, by analyzing spontaneous yawns in female groups of horses on pasture, we aim at investigating the possible presence of different morphs of yawning and which factors can influence their expression (e.g., context, age, dominance rank). As a second step, due to the horse social cohesiveness and propensity to synchronize activities and movements, we expect to find CY in our groups (*Hypothesis 1*). Moreover, in line with the *Social Modulation hypothesis*, we expect that CY is more frequent and rapid (i.e., shorter response latency), among subjects acting in a cohesive way thus sharing preferential relationships (*Hypothesis 2*).

Materials and Methods

Study area and subjects

The data collection was conducted at the Migliarino-San Rossore-Massaciuccoli Regional Park (Tuscany, Italy). This extensive reserve spans 4,800 hectares and hosts 2 distinct groups of horses with a total of 48 individuals. The study subjects were non-stable horses, living primarily in pastures, freely grazing and roaming, rather than being kept in stables or used for work in riding schools. The horses inhabit a designated area within the park, covering approximately 300 hectares, enclosed securely to prevent public access. The horses have unlimited access to water resources. When natural pasture grasses are insufficient, supplementary hay is provided. Human interactions with the animals are minimal being strictly limited to essential veterinary care. The groups included 2 breeds: the pony of Monterufoli (MR) and the Italian Heavy Draught Horse (IHD). The 2 breeds strongly differ in their body size: the height at the withers ranges from 130 to 132 cm for MR (weight range = 380–450 kg) and 155–160 cm for IHD (weight range = 700–900 kg). Both groups undergo to the same management and occupy 2 separate areas, each 1 covering 150 hectares. The MR group included 25 subjects, with ages ranging from 2 to 23 years (mean ± *SD*: 8.46 ± 3.13) and the IHD group consisted of 23 subjects, with ages ranging from 2 to 16 years (mean ± *SD*: 9.00 ± 2.84) (Table 4).

Data collection

Data collection spanned October 2021–May 2022, with video documentation conducted 5 days a week under favorable weather conditions. The initial 10 days served to habituate horses to the presence of cameras and operators. During this period horses were individually identified based on body size and external features, such as the fur color, scars, mane side, and facial traits.

To minimize any disruption to the animals' natural behavior, operators captured videos without entering the enclosure. This was possible due to the excellent visibility and by the use of Sony DSC-HX400V camera with 24× optical zoom. Stable mounts were consistently utilized for camera setups to enhance video quality. Video collection extended from 09:00 AM to 04:00 PM (individual mean hours: MR = 103.15 ± 8.66, IHD = 166.85 ± 3.37).

The concurrent presence of 2 operators allowed to gather video 1) on each focal individual to catch facial expressions including yawning and chewing and 2) at the group level, to collect data on social interactions and contexts (Altmann 1974). We conducted focal observations on all the visible subjects of the 2 groups in 10 min continuous observation sessions per individual. Each individual was observed at least twice a week since the observers passed half week with the group of MR and the other half with the group of IHD. The order of focal observations was randomized. This added up to 307 h of focal data (mean = 9.3 h/individual).

Video analyses and operational definition

Video analysis was performed using Pot-Player software, which allowed frame-by-frame scoring, including the possibility to slow down the behaviors to 70% of their original speed.

For each spontaneous yawn, the following information were recorded: 1) the identity of yawner, 2) the duration of the yawning event, 3) the visibility of teeth (teeth covered, Y_{CT} or uncovered, Y_{UCT}), 4) the exact time of the execution, and 5) the context (*solitary/social relax/social anxiety*). A yawning event started when the first frame revealed parted lips and ended when the lips appeared closed again. When a yawn was emitted by the same subject within 3 min after a previous yawn these yawning events were considered as part of a Y *chain*.

From the videos collected at the group level, we conducted a scan animal sampling every 2 min by recording the presence/absence of grooming between the dyads of animals included in the video.

Protocol to define Yawn Contagion

Horses possess a distinctive visual system that is adapted to their role as prey animals in open spaces. Their eyes are positioned laterally, providing a wide visual field of approximately 178° per side (Timney and Macuda 2001). As a result, horses are primarily monocular, with limited binocular overlap (Hanggi and Ingersoll 2012) and they have 2 completely blind spots which are limited to the front of the forehead and to the rear (Figure 1a) (Murphy et al. 2009). Moreover, horses have good visual acuity for distant objects, indicating that they are hyperopic (Murphy et al. 2009; Scopa et al. 2022). The peculiar sight of horses together with their tendency to stay in proximity with groupmates make it extremely difficult for an observer to understand if a subject had or did not have visual access to other individuals' faces. Consequently, it is challenging to know if horses detect or not the yawns performed by a trigger. For this reason, we developed a specific protocol that takes into account the visual sensory features of horses.

For this reason, each yawning event (total of 686: all the yawns recorded during social context) was systematically matched with a control condition (i.e., chewing cycle, C).

In horses, 1 chewing cycle involves 3 distinct phases (Collinson 1994; Tremaine 1997; Baker 2005): 1) in the opening stroke, the mouth movement spans from a fully closed position to a fully open position; 2) the closing stroke takes place from the fully open position to the furthest lateral (side) position with the mandible moving upwards until the lower jaw teeth make contact with the maxillary teeth; and 3) in the power stroke, the lower jaw teeth grind upon the upper jaw teeth in a lingual direction

(Staszyk et al. 2006; Bonin et al. 2007). Due to the similarity in mouth motor actions with yawning, a C cycle is an excellent behavioral control to match with a yawning stimulus. The similarity between C and Y allowed us to use 2 identical sequences of 3 movements each, except for the presence of Y: C-C-C (*Chewing condition)* and C-Y-C (*Yawning condition)*. Figure 1B represents the *Chewing condition* consisting of 3 different chewing cycles (C-C-C) and the *Yawning condition* consisting of 3 different movements, 2 chewing cycles, and 1 yawning (C-Y-C).

Each C-Y-C event was matched with a C-C-C event and the response of the visible subjects in the video was then compared. The selection of the C-C-C event was made following these criteria: same social context of the C-Y-C event (*social relax* and *social anxiety*), same number of subjects as in the previous C-Y-C event, at least 30 min far from a C-Y-C event and when animals were not feeding (since chewing could be influenced by the presence of food).

After a C-Y-C and C-C-C event, the animals in proximity to the horse emitting the previous stimulus were followed for 3 min and all the yawning events were recorded. The 3-min time window started when the trigger showed the first lip opening in the case of the *Yawning condition* and when the trigger engaged the second action of chewing of the *Chewing condition*. The limit of time to define 2 chewing cycles as separate was 10 s. Those yawning responses following the sequence C-Y-C were classified as "yawn contagion (CY)" if they occurred within a 3-min window. The 3-min criterion was selected on the basis of previous literature for comparative reasons (*Mandrillus leucophaeus*: Galotti et al. 2024; *Theropithecus gelada*: Pedruzzi et al. 2023; *Pan troglodytes*: Massen et al. 2012; Campbell and Cox 2019; *Pan paniscus* and *Homo sapiens*: Palagi et al. 2014).

Every yawn produced by the receivers within 3 min following the observation of the initial yawn was regarded as associated with it. Any yawning that occurred within this 3-min period was excluded from the calculation of spontaneous yawns. If the initial yawner displayed several yawns within the 3-min window, only the first observed yawn was considered for assessing the potential response of the receiver. This cautious method helps prevent Type I errors, though it significantly limits the sample size. The total trials were 686 C-Y-C events that were matched with 686 C-C-C events.

Latency definition

We calculated the latency between 2 yawns emitted by 2 different individuals (CY) as the difference between the first frame in which the lips of the receiver are parted and the first frame in which the lips of the trigger are parted. We considered this measure to investigate whether social factors significantly affected not only the occurrence of CY but also the response latency.

Morphology matching

For each yawning event performed by a subject B in response to a subject A, we recorded whether there was a matching of the yawn morphologies between the 2 subjects. We assigned a score of 1 when matching was present ($Y_{CT} \rightarrow Y_{CT}$ or $Y_{UCT} \rightarrow Y_{UCT}$) and 0 when it was not ($Y_{CT} \rightarrow Y_{UCT}$ or $Y_{UCT} \rightarrow Y_{CT}$). This measure was considered to investigate whether there was a reduced latency in replicating an identical yawning pattern, when a complete matching occurred.

Definition of the aggressive events

We recorded all the aggressive events to calculate the Average Dominance Index (ADI) for each subject (Table 4). The aggressive interactions included biting, kicking, chasing, attempt to bite, and dismissing. We selected only those aggressive encounters in which the winner and the looser were clearly discernible.

Contexts

We defined 3 possible contexts based on the behavior performed by the yawner immediately before and immediately after the C-Y-C/C-C-C event. We defined a *social relax* context when the yawner was in proximity of other subject/s (less than 2 body lengths far from other subjects, van Dierendonck et al. 1995; Christensen et al. 2002; Cameron et al. 2009) while resting, foraging, walking, grooming (Feh 2005; Fureix et al. 2012). We classified as a *social anxiety* context when the yawner was involved in an aggressive event or when it engaged in anxiety-releasing behavior in the previous 3 min (self-scratching; Maestripieri et al. 1992; McDonnell and Haviland 1995; Schino et al. 1996; Troisi 2002; Feh 2005; Fureix et al. 2012). Finally, the *solitary* context occurred when the yawner was alone (at least 2 body lengths far from other subjects; van Dierendonck et al. 1995; Christensen et al. 2002; Cameron et al. 2009). When the context could not be referred to any of the criteria listed above, that event was discarded.

Age categories

The age categories have been defined as follows: youngsters 2–5 years, adults 5.1–18 years, and old adults > 18 years (Lester et al. 2017). See Table 1 for details.

Grooming levels

We used grooming as a predictor of relationship quality between dyads (Goosen 1987; Fedurek et al. 2009). We counted how many scans were captured with a dyad exchanging grooming (either directional A → B, B → A, or reciprocal A ↔ B). Then, the number of scans including grooming involving A and B was divided by the number of scans including just A, just B, and A and B together.

$$\text{Grooming level} = \frac{\text{Grooming Scans}_{A\rightarrow B} + \text{Grooming Scans}_{B\rightarrow A} + \text{Grooming Scans}_{A\leftrightarrow B}}{\text{Scans}_{A} + \text{Scans}_{B} + \text{Scans}_{A+B}}$$

Kinship

We designated each pair as *kin* (coded as 1) if animals with a relatedness coefficient ranging from 0.50 (mother/offspring and siblings) to 0.25 (half-siblings and grandmother) (Wright 1922). In all the other cases the subjects were considered no-kin (coded as 0).

Frequency of yawn

In the model of the CY ($\text{MODEL}_{response}$, see below), to control for inter-individual variation in the yawning propensity, we calculated the individual hourly frequency of yawns by dividing the number of yawning events by the number of hours of observation for each individual with the following formula:

$$\text{Yawn Frequency} = \frac{\text{number of yawning events}}{\text{total observation time (h)}}$$

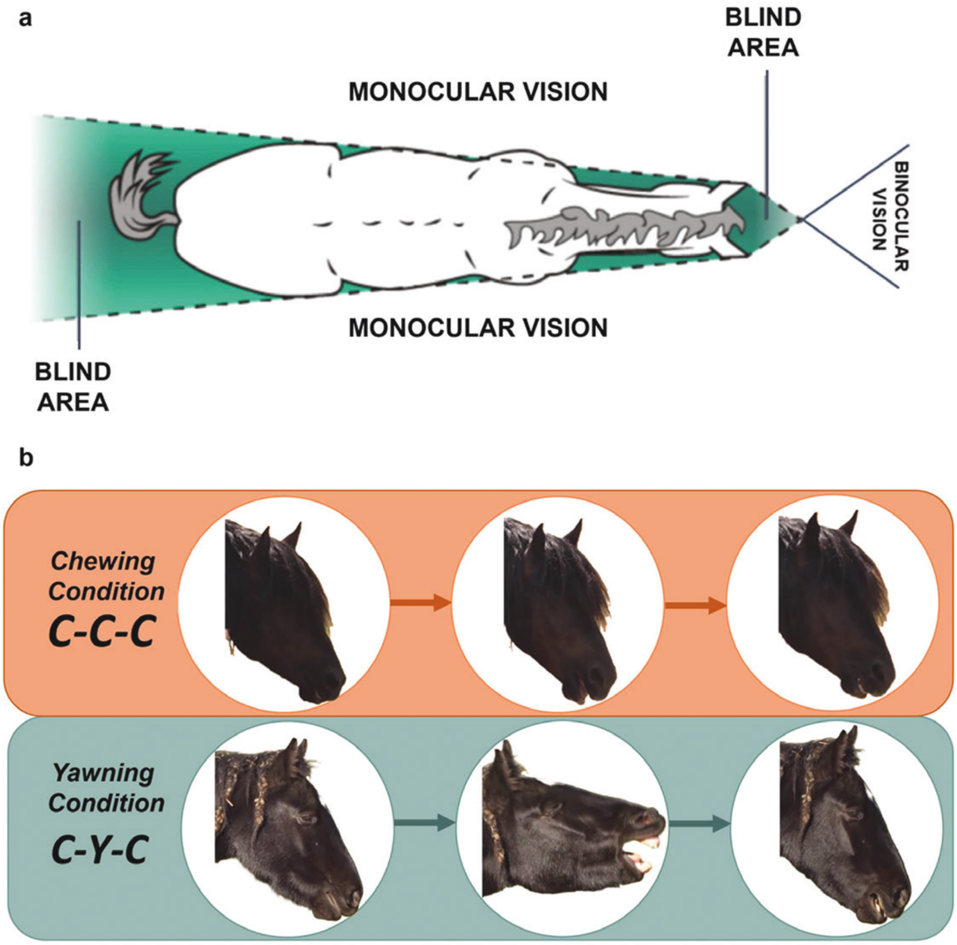


Figure 1 A) Diagram illustrating the lateral eye placement and wide visual field of approximately 178° per side in horses. B) The figure represents a diagram of the protocol that was followed to test CY. *Chewing* and *Yawning conditions* for evaluating the presence of CY in horses. The *Chewing condition* (orange) consisted in 3 different chewing movements (C-C-C) (top). The *Yawning condition* (blue) consisted in 3 different movements, 2 chewing and 1 yawning (C-Y-C) (bottom). This protocol was mandatory due to the peculiar sight of horses.

Audience

To examinate the relationship between YC and social bonds, we need to consider the probability to detect a yawn from a group member (Massen and Gallup 2017). For this reason, we defined the audience as the number of subjects that could potentially detect the stimulus; that is, the subjects who were in proximity to the yawner (less than 2 body lengths away from other subjects, as described in van Dierendonck et al. 1995; Christensen et al. 2002; Cameron et al. 2009).

EquiFACS

The Facial Action Coding System (FACS; Ekman et al. 2002) is the result of extensive research conducted by Paul Ekman and it was first published in 1978. This method describes *Action Units* (AUs) representing “the contraction of a particular facial muscle (or set of muscles) and the resulting facial movements” (Wathan and McComb 2015, p. 2) and *Action Descriptors* (ADs) representing “more general facial movements where the muscular basis either cannot be identified or is the result of a different muscle set” (e.g., deep muscles, Wathan et al. 2015, p. 2). Different FACS are now available for different animal species including horses (horses: Wathan and McComb 2015; chimpanzees: Vick et al. 2007; macaques: Parr et al. 2010; gibbons: Waller et al. 2012; orangutans: Caeiro et al. 2013; dog: Waller et al. 2013; cat: Caeiro et al. 2017; common marmoset: Caeiro et al. 2022).

The EquiFACS (Wathan et al. 2015) was applied to a subset of yawns ($N = 269$) in which the coders were able to identify the different facial muscle movements. This allowed coding for each event involving both AUs and ADs. The operators performing the analyses (the first and the second author) were official EquiFACS coders.

Reliability

The 2 operators analyzed all the videos (362 h of recordings). Before commencing coding, inter-rater reliability was checked. The 2 operators independently scored the same videos (10% of the total videos), focusing on the individual identification and the following behaviors: yawn morphology, chewing, aggressive events, grooming, contexts (*social relax, social anxiety, solitary*). The Cohen’s kappa coefficients (κ, Cohen 1960) obtained after scoring the 10% of videos were: individual identification = 0.92, yawn morphology = 0.98, chewing = 0.81, aggressive events = 0.83, grooming = 0.98, contexts = 0.91.

For every yawn configuration acquired through FACS, we computed reliability using the following equation (as recommended by the human FACS manual, Ekman et al. 2002):

$$\text{Reliability} = \frac{2\,(\text{AUs number agreed by both coders})}{(\text{AUs number coded by coder 1}) + (\text{AUs number coded by coder 2})}$$

This formula calculates the agreement for each expression with values ranging from 0 to 1 (0 = no agreement; 1 = total agreement). The average agreement between the 2 coders was 0.94 for Y_{CT} (Yawn Covered Teeth) and 0.95 for Y_{UCT} (Yawn Uncovered Teeth).

Statistical analysis

ADI

The ADI (Saccà et al. 2022) was used to calculate the individual values of the dominance rank. The index is an improvement upon Normalised David's Scores (David 1988). It has been developed to counteract significant biases when numerous dyads within groups fail to interact. To calculate ADI values, an interaction matrix was built by including all the agonistic contacts, the agonistic no-contacts, and the threat interactions. We excluded all the instances with uncertain valence, such as behaviors that were ambiguously agonistic or playful, along with mounting behaviors.

Possible presence of different yawn morphologies in horses

To systematically demonstrate the existence of different yawn morphologies in horses, we used a back-and-forth methodological approach. Initially, we categorized the morphologies a priori based on teeth visibility (Deputte 1994; Zannella et al. 2017, 2021). Subsequently, via EquiFACS we identify all the AUs, and ADs involved in each yawning event. In the initial phase, we encoded all visible AUs and ADs into a presence/absence (1/0) matrix without excluding any a priori. We then selected only the informative AUs and ADs by excluding those that were never present. Finally, an unsupervised k-means algorithm was applied to all informative AUs and ADs (excluding those present in every yawn and those in less than 5% of cases) for a hard-clustering analysis. To determine the optimal number of yawn morphologies and segment our dataset based on different combinations of AUs and ADs, we employed a *Principal Component Analysis* with mixed data. The analysis was executed on the set of AUs/ADs comprising each yawning event, utilizing the PCAmixdata package in R (Chavent et al. 2022). To validate our a priori classification of yawning morphologies, we utilized a k-means unsupervised clustering approach on the 1-hot encoded data, converting the categorical variable into a 1-hot vector representation. Given that PCA revealed 2 distinct data clusters, a k-means clustering analysis with a cluster count (k) of 2 was executed. The *Silhouette Index* up to 8 clusters was computed to verify the appropriateness of choosing 2 clusters (Rousseeuw 1987). The Exact Fisher test was applied to examine which Aus significantly differed between Y_{CT} and Y_{UCT}.

Then, we employed the NetFACS R package (Version 0.5.0, Mielke et al. 2022) to visualize the 2 different morphologies as networks. The nodes in these networks represent individual AUs/ADs linked by edges, which depict specificity probabilities. Networks are constructed by comparing the data with a null distribution built on permutations through bootstraps that re-sample the dataset. The null distribution assumes that AUs/ADs are randomly performed while maintaining the same proportion of active AUs/ADs for each data entry.

Factors possibly influencing the emission of different yawns (Y_{CT} and Y_{UCT}) ($MODEL_{morphology}$)

To understand which factors affected yawn MORPHOLOGY (Y_{CT}/Y_{UCT}) we ran a Generalized Linear Mixed Model (GLMM; glmmTMB R-package; Berry et al. 2017; Kuhn et al. 2020; Version 1.4.1717). We used MORPHOLOGY as the response variable (binomial error distribution). We included as fixed factors the CONTEXT (*solitary/social relax/social anxiety*), the ADI values of the yawner (dominance rank), the AGE CATEGORY of the yawner, and the BREED group (MR/IHD). No collinearity was found between the fixed factors (range $VIF_{min} = 1.05$; $VIF_{max} = 1.55$). The yawner identity (ID yawner) was included as a random factor.

Hypothesis 1—CY *is present in horses* ($MODEL_{response}$)

To test whether the Y response was more likely after a Yawn (*Yawning condition*) than after a Chew (*Chewing condition*), we ran a GLMM on a total of 82 events. The yawn RESPONSE (presence/absence) was the response variable (binomial error distribution). We used CONDITION (*Yawning/Chewing*), age category of the trigger (AGE_T) and receiver (AGE_R), AUDIENCE (number of subjects that could potentially detect the stimulus), YAWN FREQUENCY of the trigger and BREED group (MR/IHD) and the CONTEXT (*social relax/social anxiety*) as fixed factors. We introduced the interaction between the trigger's identity and the receiver's identity as a random factor (IDtrigger*IDreceiver). There was no evidence of collinearity among the fixed factors (range $VIF_{min} = 1.00$; $VIF_{max} = 1.24$).

Table 1. Table showing the selection of EquiFACS AUs and ADsS observed during yawning in *Equus caballus* and the comparison of AUs and ADs observed in Y_{CT} and Y_{UCT}, the relative *P*-values obtained by Fisher's exact test (significant *P*-values in bold). Y_{CT} (%) = percentage out of a total of 46 Y_{CT}; Y_{UCT} (%) = percentage out of a total of 223 Y_{UCT}

AU code	AU description	Y_{CT} (%)	Y_{UCT} (%)	*P* values
AU10	Upper lip raiser	0 (0)	222 (0.99)	**<0.001**
AU16	Lower lip depressor	1 (0.02)	177 (0.79)	**<0.001**
AU25 + 26	Lips part + jaw drop	42 (0.91)	3 (0.01)	**<0.001**
AU25 + 27	Lips part + mouth stretch	4 (0.08)	220 (0.98)	**<0.001**
AU101	Inner brow raiser	19 (0.41)	96 (0.43)	0.871
AU122	Upper lip curl	0 (0)	135 (0.60)	**<0.001**
AU143	Eye closure	5 (0.10)	170 (0.76)	**<0.001**
AU145	Blink	22 (0.47)	22 (0.09)	**<0.001**
AD1	Eye white increase	4 (0.08)	17 (0.07)	0.765
AD19	Tongue show	6 (0.13)	52 (0.23)	0.167
AD30	Jaw sideways	18 (0.39)	150 (0.67)	**0.001**
AD38	Nostril dilator	42 (0.91)	165 (0.73)	**0.011**
AD57	Nose forward	21 (0.45)	178 (0.79)	**<0.001**
EAD101	Ears forward	17 (0.36)	102 (0.45)	0.328
EAD103	Ears flattener	1 (0.02)	30 (0.13)	**0.038**
EAD104	Ear rotator	29 (0.63)	89 (0.39)	**0.005**

Hypothesis 2—*Relationship quality affects the occurrence (MODEL$_{occurrence}$) and latency of CY (MODEL$_{latency}$)*

Considering the *Yawning condition*, we investigated which factors affected the occurrence of CY when we ran a GLMM. The presence/absence of yawning RESPONSE was the response variable (binomial error distribution). The fixed factors were ADI value of the trigger (ADI$_T$) and ADI value of the receiver (ADI$_R$), CONTEXT (*social relax*/*social anxiety*), MORPHOLOGY (Y$_{UCT}$/Y$_{CT}$), dyadic GROOMING, KINSHIP (0/1) between the trigger and the potential responder and interaction between the last 2 factors (GROOMING*KINSHIP). The interaction between the identity of the trigger and receiver was inserted as a random factor (ID$_{trigger}$*ID$_{receiver}$). No collinearity was found between the fixed factors (range VIF$_{min}$ = 1.01; VIF$_{max}$ = 2.74).

We also investigated the latency of CY response by running an LMM. The LATENCY (*cs*) of response was the response variable (Gaussian error distribution). By looking at the Q-Q plot and plotting the residuals against the fitted values we verified the normal distribution and the homogeneity of the model residuals (Estienne et al. 2017). The fixed factors were dyadic GROOMING, KINSHIP (0/1) between the trigger and the potential responder and interaction between the last 2 factors (GROOMING*KINSHIP), ADI values, CONTEXT, yawn MORPHOLOGY, and the MORPHOLOGY MATCHING ($Y_{CT} \rightarrow Y_{CT}$ or $Y_{CT} \rightarrow Y_{UCT}$—$Y_{UCT} \rightarrow Y_{CT}$ or $Y_{UCT} \rightarrow Y_{UCT}$). The interaction between the identity of the trigger and receiver was inserted as a random factor (ID$_{trigger}$*ID$_{receiver}$).

No collinearity was found between the fixed factors (range VIF$_{min}$ = 1.05; VIF$_{max}$ = 1.55).

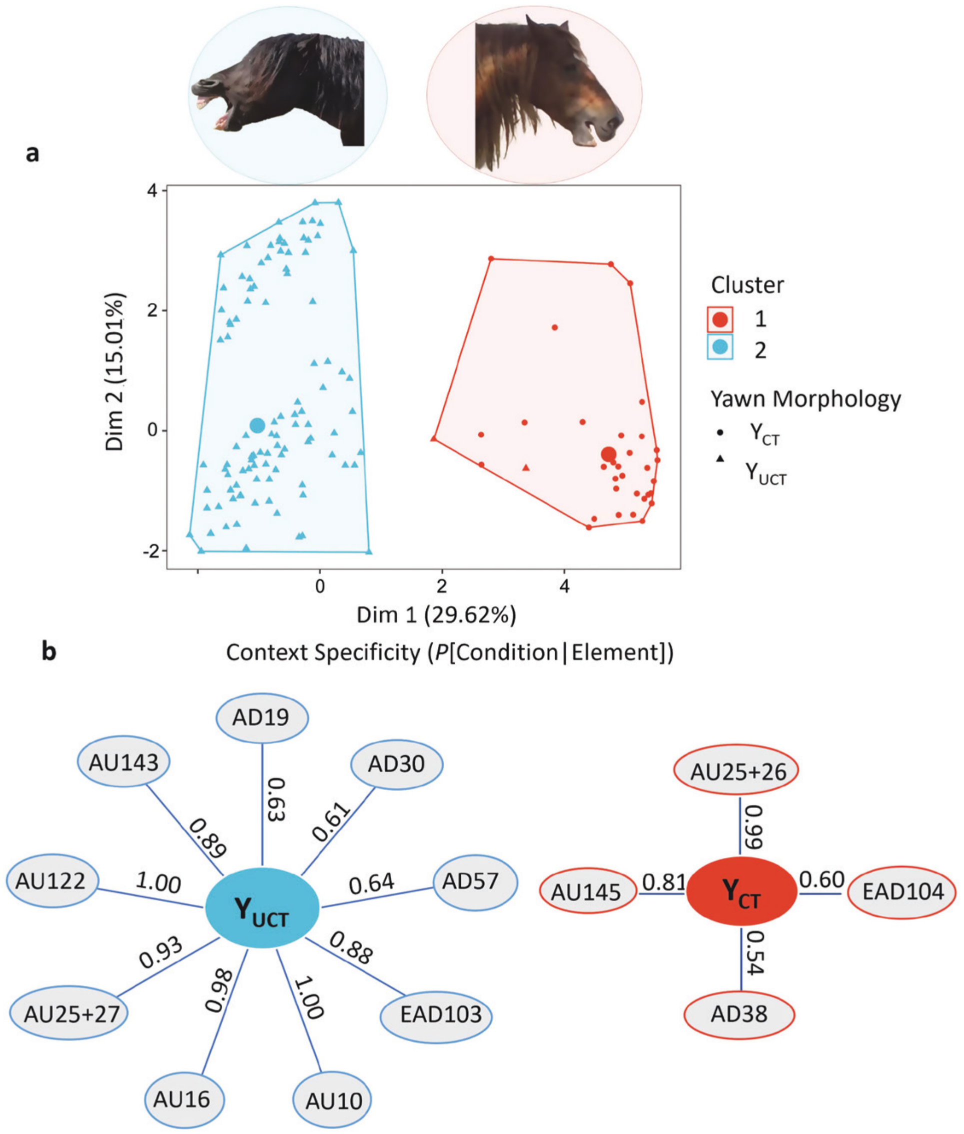


Figure 2 A) A visual representation of the entire set of yawns is constructed by applying Principal Component Analysis of mixed data (PCAmix), combined with the integration of k-means clustering results. The different shapes of the points on the map, indicated by circles and triangles, correspond to the predefined classifications of Y_{UCT} (N = 223, on the left) and Y_{CT} (N = 46, on the right). Within the clusters identified by k-means, the red and blue clusters delineate the distribution of Y_{CT} and Y_{UCT}, respectively. Dim 1 (29.62%) and Dim 2 (15.01%) provide a condensed representation of the original variables, akin to a projection or "shadow" of the original dataset. Each dimension captures a distinct portion of the variability, representing valuable information from the original dataset. B) Network illustrating the probability of Y_{UCT} (blue) and Y_{CT} (red) occurrence when an AU was active (only P values < 0.01 are shown).

By using a likelihood ratio test (LRT, Anova with argument test “Chisq”; Dobson and Barnett 2018), we tested the significance of the full model (Forstmeier and Schielzeth 2011) by comparing it against a null model ($MODEL_{morphology}$/$MODEL_{response}$/$MODEL_{occurence}$/$MODEL_{latency}$). Then, the *P*-values for the individual predictors were calculated based on the LRTs between the full and the null/control model by using the R-function *Anova* in the R-package *car* 3.0–10 (Fox and Weisberg 2019). The marginal R^2, which represents the variance explained by fixed factors only, and the conditional R^2, which represents the variance explained by the entire model, including fixed and random effects (Nakagawa et al. 2017), were calculated using the R-package MuMIn (Version 1.43.17, Bartoń 2020).

Results

ADI

Table 1 contains the ADI values for each individual.

Presence of different yawn morphologies in horses

We collected a total of 743 spontaneous yawns excluding the case considered as CY (Yawn Covered Teeth, $Y_{CT} = 175$; Yawn Uncovered Teeth, $Y_{UCT} = 568$; 686 under social context and 57 under solitary context) on 1 group of ponies of Monterufoli (MR, $N_{MR} = 18$; $N_{yawns} = 248$) and 1 group of Italian Heavy Draught horse (IHD, $N_{IHD} = 15$; $N_{yawns} = 495$). From this sample, we extracted and codified via Facial Action Coding System (FACS) both Y_{CT} ($N = 46$, from 19 individuals) and Y_{UCT} ($N = 223$, from 28 individuals). The a priori identification of Y_{CT} and Y_{UCT} was confirmed by the k-means unsupervised clustering analysis. For the Y_{CT} data clustered in the 100% of cases. For the Y_{UCT} 96% of cases clustered in the a priori-defined classification and 4% clustered in the Y_{CT} group (Figure 2A). The different AUs and the ADs recorded during the entire execution of Y_{CT} and Y_{UCT} and the results of the Exact Power Fisher test are reported in Table 2.

To investigate the correlation between AUs and ADs with Y_{CT} and Y_{UCT}, we performed a network analysis by the NetFACS package (NetFACS, Mielke et al. 2022) (See Table 2 for definition of each AUs and ADs). This involved assessing the likelihood of each AU and AD being present in each yawning event. Our results showed that AU25 + 26 (0.99, $P < 0.01$), AU145 (0.81, $P < 0.01$), AD38 (0.54, $P < 0.01$), and EAD104 (0.60, $P < 0.01$) exhibited a higher probability of association with Y_{CT}. In contrast, Y_{UCT} was significantly more likely to be associated with AU10 (1.00, $P < 0.01$), AU16 (0.98, $P < 0.01$), AU25 + 27 (0.93, $P < 0.01$), AU122 (1.00, $P < 0.01$), AU143 (0.89, $P < 0.01$), AD19 (0.63, $P < 0.01$), AD30 (0.61, $P < 0.01$), AD57 (0.64, $P < 0.01$) and EAD103 (0.88, $P < 0.01$). See Figure 2B.

Table 2. Estimated parameters (Coeff), standard error (*SE*), and results of the LRTs (χ^2) of the $MODEL_{morphology}$. Significant *P* values are shown in bold; *df* = degree of freedom; n/a = not applicable

Which factors influence the emission of different yawns ($MODEL_{morphology}$)

Fixed effects	Coeff	*SE*	χ^2	*df*	*P*
Intercept	0.455	0.771	n/a	n/a	n/a
Age category			0.291	2	0.864
Adult	0.297	0.706			
Old adult	0.432	0.809			
Context			4.094	2	0.129
Social relax	0.704	0.351			
Social anxiety	0.721	0.417			
Breed	−0.969	0.329	8.666	1	**0.003**
ADI_{CAT}	0.764	0.514	2.205	1	0.137

Variance for the random factors: random $ID_{yawner} = 0.173 \pm 0.416SD$. Marginal $R^2 = 0.06$; Conditional $R^2 = 0.11$; $N_{observation} = 743$; $N_{yawner} = 33$.

Factors possibly influencing the emission of different yawns (Y_{CT} and Y_{UCT}) ($MODEL_{morphology}$)

The full model built to investigate which factors influenced the yawn MORPHOLOGY (Y_{CT}/Y_{UCT}) significantly differed from the null model (LRT: $\chi^2 = 16.336$, $df = 6$, $P = 0.012$; Table 3). In particular, we found that the CONTEXT (solitary/social relax/social anxiety), the AGE_{CAT} (youngsters, adults, old adults) of the yawner, and the dominance rank (ADI) had no significant effect on the response variable (Table 2). The BREED group (MR/IHD) significantly affected the yawn MORPHOLOGY, with MR horses engaging in more Y_{UCT} than IHD horses (Figure 3).

Hypothesis 1—CY is present in horses ($MODEL_{response}$)

The full model built to investigate whether the yawn RESPONSE (presence/absence) was more likely after a *Chewing-Yawn-Chewing* event (C-Y-C) than after a *Chewing-Chewing-Chewing* event (C-C-C) and significantly differed from the control model. The control model included the age category of the trigger (AGE_T) and receiver (AGE_R), AUDIENCE (number of subjects that could potentially detect the stimulus), YAWN FREQUENCY of the trigger, BREED group (MR/IHD) and the CONDITION (*social relax/social anxiety*) except the CONDITION (*Yawning/Control*) (LRT: $\chi^2 = 65.817$, $df = 1$, $P < 0.001$; Table 4). The results show that the probability to obtain a yawn response under the *Yawning condition* (C-Y-C) was higher than in the *Chewing condition* (C-C-C). Specifically, in the *Yawning condition* there was an 88.3% likelihood of yawning in response to another yawn (102 cases), with only an 11.7% response rate in the *Chewing condition* (3 cases) (Figure 4).

Hypothesis 2—Relationship quality affects the occurrence ($MODEL_{occurrence}$) and latency of CY ($MODEL_{latency}$)

The full model built to investigate if the relationship quality affected the occurrence of CY events did significantly differ from the control model (LRT: $\chi^2 = 19.193$, df = 6, $P = 0.004$; Table 4). ADI value of the trigger (ADI_T), ADI value of the receiver (ADI_R), dyadic GROOMING, KINSHIP (0/1) between the trigger and the potential responder and interaction between the last 2 factors (GROOMING*KINSHIP) were considered as fixed variables and CONTEXT (*social relax/social anxiety*), MORPHOLOGY (Y_{UCT}/Y_{CT}), were included in both the null and the control model. While ADI_T and ADI_R did not influence the occurrence of CY, the variables KINSHIP and GROOMING had a significant affect (Table 3). Horses responded more likely to kin than non-kin subjects (Figure 5A) and to subjects with whom they shared higher grooming frequency (Figure 5B). The interaction KINSHIP*GROOMING was not significant.

Table 3. Estimated parameters (Coeff), standard error (*SE*), and results of the LRTs (χ^2) of the MODEL$_{\text{response}}$, MODEL$_{\text{occurrence}}$, and MODEL$_{\text{latency}}$. Significant *P* values are shown in bold; *df* = degree of freedom; n/a = not applicable

Fixed effects	Coeff	*SE*	χ^2	*df*	*P*
Hypothesis 1 (GLMM) - Contagious yawning (MODEL$_{\text{response}}$)[a]					
Intercept	−6.742	1.298	n/a	n/a	n/a
Tested variable					
Condition	2.118	0.325	42.283	1	**<0.001**
Control variables					
Age$_T$	0.987	0.426	5.358	1	**0.020**
Age$_R$	0.244	0.417	0.342	1	0.558
Audience	−0.064	0.155	0.173	1	0.677
Breed group	−0.097	0.319	0.093	1	0.759
Yawn frequency	−1.257	1.249	1.013	1	0.314
Context	−0.265	0.365	0.528	1	0.467
Hypothesis 2 (GLMM) - Relationship quality affects the occurrence of YC (MODEL$_{\text{occurrence}}$)[b]					
Intercept	−3.957	0.649	n/a	n/a	n/a
Tested variables					
Grooming	2.325	2.167	5.455	1	**0.019**
Kinship	0.596	0.307	6.332	1	**0.011**
Grooming*Kinship	1.830	2.894	0.399	1	0.527
Control variables					
ADI$_T$	0.743	0.621	1.432	1	0.231
ADI$_R$	1.313	0.715	3.371	1	0.066
Context	−0.520	0.389	1.783	1	0.182
Morphology	−0.344	0.280	1.507	1	0.219
Hypothesis 2 (GLMM) - Relationship quality latency of YC (MODEL$_{\text{latency}}$)[c]					
Intercept	92.379	26.667	n/a	n/a	n/a
Tested variables					
Grooming	209.382	105.510	0.331	1	0.564
Kinship	−2.390	16.382	5.805	1	**0.015**
Grooming*Kinship	−522.134	212.014	6.065	1	**0.013**
Control variables					
ADI$_T$	−16.362	27.391	0.356	1	0.550
ADI$_R$	−29.678	29.766	0.994	1	0.318
Morphology	4.044	11.886	0.115	1	0.733
Morphology matching	−20.219	11.722	2.975	1	0.084
Context	−10.011	19.978	0.251	1	0.616

[a] Variance for the random factors: ID$_{\text{receiver}}$ = 0.255 ± 0.505*SD*; random ID$_{\text{trigger}}$ = 0.015 ± 0.123*SD*. Marginal R^2 = 0.26; Conditional R^2 = 0.32; $N_{\text{observation}}$ = 2392; N_{receiver} = 32; N_{trigger} = 32.

[b] Variance for the random factors: ID$_{\text{receiver}}$ = 0.432 ± 0.658*SD*; random ID$_{\text{trigger}}$ = 0.213 ± 0.461*SD*. Marginal R^2 = 0.09; Conditional R^2 = 0.24; $N_{\text{observation}}$ = 1196; N_{receiver} = 32; N_{trigger} = 32.

[c] Variance for the random factors: ID$_{\text{receiver}}$ = 0.173 ± 0.413*SD*; random ID$_{\text{trigger}}$ = 456.600 ± 21.370*SD*. Marginal R^2 = 0.21; Conditional R^2 = 0.54; $N_{\text{observation}}$ = 83; N_{receiver} = 25; N_{trigger} = 25.

The full model built to investigate if the KINSHIP, GROOMING, and KINSHIP*GROOMING affected the LATENCY of CY significantly differed from the control model (LRT: χ^2 =16.336, *df* = 6, *P* = 0.012; Table 4) including ADI$_T$, ADI$_R$, CONTEXT, MORPHOLOGY and MORPHOLOGY MATCHING (matched: $Y_{CT} \rightarrow Y_{CT}$ or $Y_{CT} \rightarrow Y_{UCT}$; no-matched: $Y_{UCT} \rightarrow Y_{CT}$ or $Y_{UCT} \rightarrow Y_{UCT}$) as fixed factors. The variable KINSHIP significantly affected the response latency with kin being more rapid in the Y response (Table 3, Figure 6A). While GROOMING did not affect the response latency, the KINSHIP*GROOMING had a significant effect on the response variable with more rapid responses in kin subjects that spent more time grooming each other (Figure 6B, Table 4).

Discussion

Despite the highly stereotyped nature of yawning, universally considered as an excellent example of *fixed action pattern*, there are some differences in the way this behavior can be displayed (Provine 2005). It has already been demonstrated in several primate species that different morphs of yawn exist (Vick and Paukner 2010; Leone et al. 2014; Zannella et al. 2021; Galotti et al. 2024). Yawning in herbivores is still neglected with no studies on yawning in ungulates investigating its variability. Via EquiFACS we tested whether a priori distinction of 2 different yawn morphologies based on teeth visibility (Yawn Uncovered Teeth, Y_{UCT}; Yawn Covered Teeth, Y_{CT}, Supplementary Figure S1) was reliable. By analyzing a subset of well-visible yawns, our results confirm that horses show 2 distinct yawn morphologies (Figure 2A) as it has been found in social primates (Vick and Paukner 2010; Zannella et al. 2021; Galotti et al. 2024). Through a network analysis (NetFACS) we assessed the likelihood of each AU and AD being present in each yawning event showing that Y_{UCT} was associated with 9 AUs/ADs, while Y_{CT} with 4 AUs/ADs (Figure 2B). The total absence of AU overlapping and the higher number of AUs recruited during Y_{UCT} suggest that this form of yawn is more complex than Y_{CT}. In addition, our results can have a direct application. When it is difficult to obtain videos of good quality due to challenging observational settings, teeth visibility per se can be used to discriminate different morphs of yawns, thus providing a useful tool in yawning investigation.

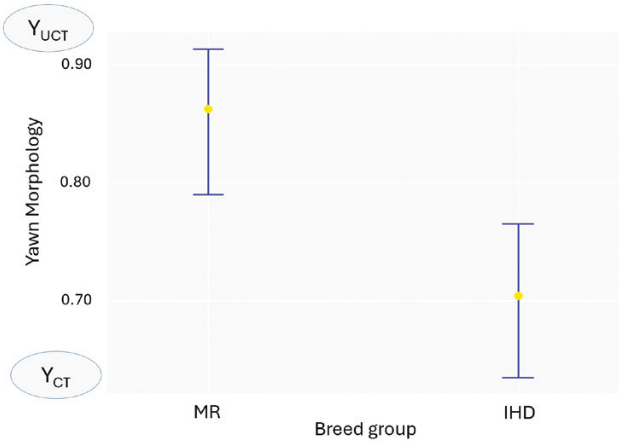


Figure 3 Barplot showing the effect of breed group (MR = pony of Monterufoli, IHD = Italian Heavy Draught Horse) on Yawn Morphology (Y_{UCT}/Y_{CT}).

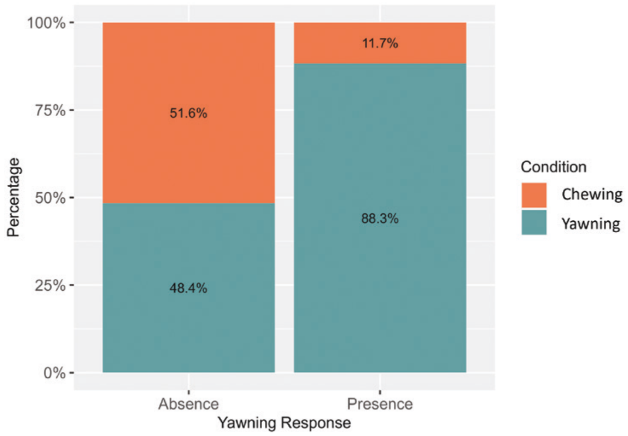


Figure 4 Graph illustrating the percentages of absence and presence of yawning response in the *Yawning condition* (blue) and *Chewing condition* (orange) ($N_{observations} = 686$, $N_{Yresponse} = 102$, and $N_{Cresponse} = 3$).

Yawning may have communicative functions (Guggisberg et al. 2010) especially in those species that live in large social groups and with complex social dynamics, as horses (Maeda et al. 2021). In this perspective, in primates, different yawn morphologies have been found to be associated with different social contexts (*Theropithecus gelada*, Leone et al. 2014; *Pan troglodytes*, Vick and Paukner 2010; *Macaca tonkeana*, Zannella et al. 2017). Contrary to other studies, we did not find any influence of the imminent individual context (social or solitary) on the emission of the different types of yawns. This could be related to the limitation of our study groups including only adult females with their offspring. Contrary to the agonistic encounters involving stallions (Olczak and Klocek 2014), female agonistic interactions mostly involve threatening actions probably provoking less anxiety variations in animals. Indeed, a study on Przewalski horses showed that after agonistic interactions, stallions yawned more than females (Górecka-Bruzda et al. 2016).

If the context did not apparently influence the different yawn morphologies, the breed seems to have a role, with ponies of Monterufoli performing more Y_{UCT} compared to Italian Heavy Draft horses (Figure 3). Although, the interpretation

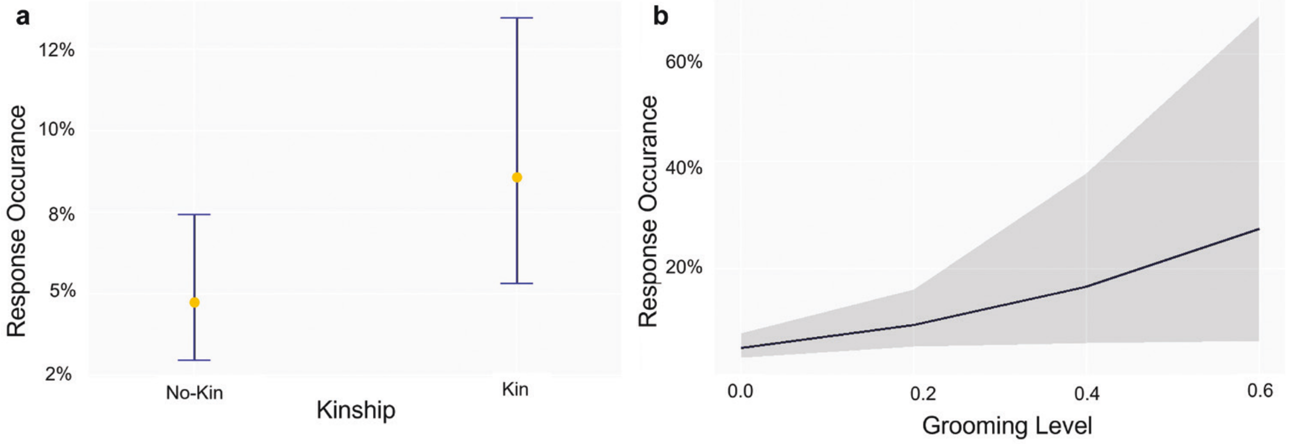


Figure 5 A) Barplot depicting the effect of kinship (No-Kin/Kin) on the frequency of YC events. B) Effect plot showing the positive covariance between grooming levels and the frequency of CY shared by the interacting horses.

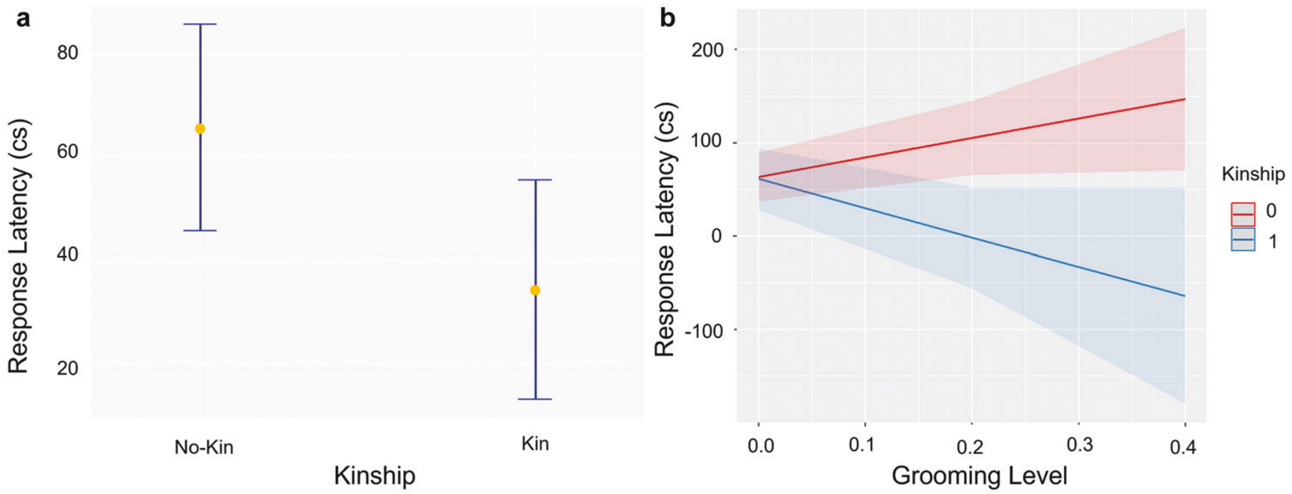


Figure 6 A) Barplot depicting the effect of kinship (No-Kin/Kin) on the latency of CY responses (in seconds). B) Effect plot showing the effect of the interaction between grooming and kinship on the time latency of CY.

of this outcome is anything but straightforward, a possible explanation can be found in the *Brain Cooling Hypothesis* (Gallup et al. 2016; Massen et al. 2021). We could hypothesize that to cool a relatively larger brain, the animal can display larger yawns (Galotti et al. 2024). Shetland ponies have been observed to have a number of distinctive cranial features, including a broad skull with a rounded ribcage, a concave face, and large orbits, all characteristics predictive of a larger brain compared to other breeds of horses (Hanot et al. 2021). These traits, that are typical of the juvenile phases in horses, are retained in pony adults probably due to a pedomorphosis phenomenon (Goodwin et al. 2008). In short, ponies manifest larger skulls compared with the body size even as adults (Hanot et al. 2021). The higher frequency of Y_{UCT} displayed by the pony of Monterufoli could be an indirect cue supporting the *Brain Cooling Hypothesis* (Gallup et al. 2016; Massen et al. 2021), although it remains highly speculative.

Some authors state that the social value of yawning is a derived feature, while the primitive function of yawning is mainly physiological (Gallup 2011; Palagi et al. 2020). One of the most relevant results of our study is the demonstration of CY in horses (Figure 4). Since CY can have a role in social and motor coordination (Casetta et al. 2021; Gallup 2022), our finding fits with the high level of group cohesion of this species (Maeda et al. 2021). The possible role of CY in favoring inter-individual cohesiveness is supported by the data showing that our mares were more likely to respond to kin compared to non-kin (Figure 5A) and to groupmates with whom they frequently engaged in mutual grooming (Figure 5B). On the other side, CY was not affected by the mares' dominance rank. Females remain in their natal groups throughout their entire lives allowing them to form long-term bonds resulting in coordinated movements during their daily activities and active participation in affiliative exchanges, such as mutual grooming (Arnold and Grassia 1982; Waring 1983; Keiper and Sambraus 1986). Among mares, dominance ranks do not shape mutual grooming thus making the mares' society highly fluid from a social viewpoint (Kimura 1998). Hence, the social modulation of CY reflects the sociobiology of the species with a possible role to increase synchronization of social activities that do not seem to be mediated by dominance relationships.

Although some empirical data indicate that CY helps synchronize activities and not viceversa (lions, Casetta et al. 2021; humans, Gallup and Meyers 2021), the potential impact of circadian rhythms on the synchronization of yawns cannot be discounted (Massen et al. 2017). The tendency of social animals to engage in shared activities, such as waking, feeding, and resting, leads to the alignment of their circadian rhythms. It is a reasonable hypothesis that spontaneous yawns cluster temporally within social groups, due to the alignment of their circadian rhythms. This could explain why yawns occur in rapid succession and, unlike chewing events, may be attributed to both contagion and common neurophysiological changes, such as fluctuations in brain or body temperature (Landolt et al. 1995). Additionally, kinship and grooming can facilitate the synchronization among socially bonded animals (Massen and Gallup 2017; Gallup 2022).

To promptly synchronize their activities, humans and non-human animals need to rapidly change their behavior according to others' (Nagasaka et al. 2013; Hattori 2021). CY was faster in mares that were kin compared to non-kin (Figure 6A) and reached the lowest latency response between kin mares who mostly groomed each other (Figure 6B). disen Data on humans (Gallup and Meyers 2021) and social carnivores (Casetta et al. 2021) indicate that perceiving a yawn from a conspecific increases the alertness state in the receiver that will be more prone to respond in a congruent and rapid way. From an evolutionary viewpoint, the ability to respond more and faster to familiar yawns can provide selective advantages due to an increased behavioral coordination. This hypothesis needs to be addressed in future studies where the temporal relation between the CY event and the subsequent behavioral alignment of the 2 interacting agents should be evaluated. We are confident that expanding the exploration of yawning to other ungulate social species living in complex societies can open new scenarios on the functions of spontaneous yawning, CY, and their predictable immediate consequences for the social partners.

Limitations of the study

Exploring the possible social functions of yawning and CY is challenging per se, but it can be even more challenging in

Table 4. The group composition. Total observation time expressed in hours. Age categories are 1 = youngsters, 2 = adults, and 3 = old adult (Lester et al. 2017). Number of Y_{CT} and Y_{UCT} for each individual and the frequency of yawns per hour. ADIvalues = values obtained via ADI procedure; Y_{CT} = yawn with covered teeth; Y_{UCT} = yawn with uncovered teeth. The asterisks (*) indicate missing values for the exact names of the mother and father, but it is certain that any unknown parent was not related to the other subjects in the group

Name	Age (year)	Age category	Mother	Father	Number Y_{CT}	Number Y_{UCT}	Frequency yawns (Y/h)	Breed	ADI
F1	10	2	Vera	Zar	11	15	0.148	IHD	0.665
E1	11	2	Vera	Zar	8	20	0.161	IHD	0.875
D1	12	2	Vera	Zar	13	19	0.187	IHD	0.750
M1	6	2	Brenta	Zar	7	14	0.132	IHD	0.277
B1	14	2	*	Gonzalez	8	29	0.251	IHD	0.999
D2	12	2	Mammola	Requaro	12	47	0.338	IHD	0.625
N1	5	1	Bimba	Zar	5	23	0.183	IHD	0.092
M2	6	2	Cicala	Zoran	6	7	0.085	IHD	0.205
B2	14	2	Sistina	Requaro	11	58	0.387	IHD	0.687
I1	8	2	Carla	Zar	18	19	0.221	IHD	0.557
B3	14	2	Vera	Zar	14	48	0.329	IHD	0.857
F2	10	2	Brenta	Gonzalez	5	14	0.111	IHD	0.909
E2	11	2	Quintilla	Requaro	10	31	0.218	IHD	0.507
M3	6	2	Ambra	Zar	13	10	0.149	IHD	0.269
I2	8	2	Brina	Zoran	12	29	0.265	IHD	0.307
L1	2	1	Veliana	Edolo	1	3	0.121	MR	0.906
L2	2	1	Umberta	Edolo	0	4	0.121	MR	0.775
L3	2	1	Dea	Kornos	3	7	0.303	MR	0.733
C1	7	2	Umberta	Eusebio	6	38	0.320	MR	0.031
V1	17	2	*	*	1	15	0.118	MR	0.458
C2	7	2	Ulrica	Eusebio	2	6	0.057	MR	0.888
U1	18.5	3	*	*	1	19	0.148	MR	0.618
F3	5	1	Veliana	Edolo	3	2	0.151	MR	0.146
D3	6	2	*	*	1	3	0.121	MR	0.222
D4	6	2	*	*	1	3	0.121	MR	0.667
Z1	16	2	Birba	*	4	16	0.148	MR	0.416
E3	6	2	Rebecca	Edolo	1	10	0.333	MR	0.417
I3	4	1	Ulrica	*	0	6	0.181	MR	0.667
A1	9	2	Ulrica	Eusebio	7	14	0.159	MR	0.289
R1	20	3	*	*	0	14	0.106	MR	0.916
U2	18.5	3	*	Baldo	7	16	0.170	MR	0.614
V2	20	3	*	*	0	3	0.022	MR	0.786
E4	10	2	Belinda	Montenero	4	54	0.433	MR	0.474

domestic species which often live under strict human management. Focusing on horses living in steady social groups offers unique opportunities to investigate the yawing phenomenon. However, the inclusion of stallions in these groups is typically difficult due to management constraints, often involving the periodic removal and reintroduction of stallions depending on the period. Hence, one of the limitations of our study is that the sample includes only mares thus preventing to take under consideration all the social dynamics of a natural social group. Although this study reveals that in horses CY positively covariates with the social linkage between the interacting subjects, we are still far to understand how CY fine-tune social interactions in this species.

Acknowledgments

The authors express their gratitude to Riccardo Gaddi and Lorenzo Bani, Director and President of the Parco Regionale Migliarino, San Rossore—Massaciuccoli, for granting permission to conduct this study. We also extend our heartfelt appreciation to all staff members of the Park whose unwavering assistance and logistical support were indispensable throughout the observation period. Without their help this study would not have been feasible.

Authors’ Contributions

A.G. and E.P. conceived the study; A.G., M.R. collected the data; M.R. performed the video analyses; A.G. performed the statistical analyses; A.G. and E.P. drafted the manuscript; A.G., M.R., P.B. and E.P. revised the final version of the manuscript.

Conflict of Interest statement

The authors declare that they have no conflict of interest.

Ethics Statement

The research was entirely observational and did not involve the manipulation of horses. As a result, the *Animal Care and Use Committee* of the University of Pisa waived the requirement for approval.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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