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Eye white may indicate emotional state on a frustration–contentedness axis in dairy cows

A.I. Sandem^{a,*}, B.O. Braastad^a, K.E. Bøe^b

^a*Department of Animal Science, Agricultural University of Norway, P.O. Box 5025, N-1432 Ås, Norway*

^b*Department of Agricultural Engineering, P.O. Box 5065, N-1432 Ås, Norway*

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Abstract

Research on welfare indicators has focused primarily on indicators of poor welfare, but there is also a need for indicators that can cover the range from good to poor welfare. The aim of this experiment was to compare behaviour elements in dairy cows shown in response to a frustrative situation as well as elements shown as a response to pleasant, desirable stimuli, and in particular measure the visible percentage of white in the eyes. The subjects of the study were 24 randomly selected dairy cows, 12 in each group, all Norwegian Red Cattle. In a 6 min test of hungry cows, access to food and food deprivation were used as positive and frustrating situations, respectively. The cows of the positive stimulus group were fed normally from a rectangular wooden box. When the deprived animals were introduced to the stimulus, the box had a top of Plexiglas with holes so that the cows could both see and smell the food, but were unable to reach it. All cows were habituated to the box before the experiment started. All food-deprived cows showed at least one of these behaviours: aggressiveness (the most frequent), stereotypes, vocalization, and head shaking, while these behaviour patterns were never observed among cows given food. The percentage of white of the total visible eye area was larger than normal in the food-deprived cows, gradually increasing until 4 min after test starts, while it was consistently lower than normal in the cows that were fed. The percentage of white correlated positively with the number of aggressive butts in deprived cows. The results suggest that the eye white may be a dynamic indicator of emotions in dairy cattle on a frustration–contentedness axis.

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* Corresponding author. Tel.: +47-64-94-80-73, fax: +47-64-94-79-60.

E-mail address: agnethe-iren.sandem@ihf.nhl.no (A.I. Sandem).

1. Introduction

Consumers of animal products increasingly demand that animals are reared, transported and handled in a humane way. On-farm welfare assessment must be based on validated welfare indicators that are simple enough to be used by the farmer in his ethical quality assurance of the animal production, and by veterinarians and official animal welfare committees that supervise animal productions.

Despite different definitions, to be concerned about animal welfare is to be concerned with the subjective feelings of animals (Dawkins, 1988). However, most subjective feelings tentatively identified in research until now can be categorized as negative, e.g. related to suffering, stress, and pain (Dawkins, 1980; Baxter, 1983; Van Rooijen, 1984; Zayan and Duncan, 1987). These are indicators of the absence of welfare, they indicate that the individual cannot cope with current conditions or environmental challenges (Spruijt et al., 2001). Welfare should be defined from the individual animal's perspective as the positive balance between positive (reward) and negative (aversive events) experiences. Few studies have been concerned with pleasant feelings and positive welfare indicators.

In addition to the manifestation of a full behaviour repertoire (Hughes, 1988), one of the few positive welfare indicators suggested is play behaviour. This may be used to indicate good welfare in calves and juveniles of other farm animal species (Jensen et al., 1998). There is however a need for developing reliable indicators of good welfare in adult cows.

Preliminary studies indicated that wide-open eyes might be an emotional indicator in cows. As far as we know, observations of the percentage of white in the eyes are not previously described as a welfare indicator in cattle or other species. A pilot study on a few cows indicated that there were differences respecting the percentage of visible white in the eyes when cows were introduced to frustrative and rewarding food stimuli. More of the white appears when especially the upper eyelid is lifted. The sympathetic nervous system might be involved in this response. Sympathetic postganglionic axons originating in the cranial cervical ganglion in the anterior neck course to the region of the eye where they innervate the dilator fibers of the iris, providing the well-known pupil dilatation during acute stress, as well as innervating the muscle that helps lift the upper eyelid and the muscle that keeps the nictitating membrane (third eyelid) in place at the medial canthus of the eye (Cunningham, 1997). We therefore wanted to investigate to what extent the percentage of white in the eyes can reflect responses to frustrating and rewarding food stimuli, in situations that might affect the sympathetic nervous system.

In order to validate the relevance of this parameter to animal welfare, we decided to observe other generally accepted welfare indicators as well: stereotypies, vocalizations, and aggressive behaviour. The most common stereotypies shown by cattle are tongue rolling, bar biting and licking of equipment (Sambras, 1985; Wiepkema, 1987). Stereotypy performing animals are generally subject to, or have been exposed to, long-lasting frustrating situations (Redbo, 1990), and exhibiting stereotypies is generally thought to indicate poor welfare (Broom, 1983, 1991). Vocalization may sometimes indicate stress. Cattle that were inverted onto their backs in commercial slaughter plants had significantly higher cortisol levels and more vocalizations per animal compared to cattle held in an upright position (Dunn, 1990). According to Watts and Stookey (2000), vocal behaviour in cattle is the animal's commentary on its biological status and welfare. High frequency of

aggression may also indicate poor welfare (Duncan and Wood-Gush, 1971; Carlstead, 1986). Aggression may reflect an animal's attempt to avoid or alleviate negative situations. Nielsen et al. (1997) found that the incidence of aggression in group housed heifers decreased in an experiment where the bedded lying area was increased from 1.8 to 2.7 m per heifer.

The general aim of our study was to find and describe behaviour traits in cattle that can reflect the cows' subjective emotions. Consequently, we wanted to identify behaviour elements shown as a response to pleasant (positive) stimuli as well as elements shown as a response to frustrating (negative) stimuli. In the present study we predicted the visible percentage of white in the eye to be higher than normal when cows were thwarted from access to food and lower than normal when they got access to food. Other behavioural welfare indicators should be expected to correlate with the percentage of white in the eyes.

2. Material and methods

2.1. *Animals and housing*

The subjects were 24 randomly selected commercial dairy cows (Norwegian Red Cattle). The cows in the experiment were between 2 and 6 years old, averaging 3.5 years. They were housed in a tie stall system, in a barn containing 90 cows in total. The animals were on pasture from May till September. They were fed with two meals of 10–20 kg grass silage and four meals of 1.5–3 kg concentrate the rest of the year. Water was available *ad libitum*. The recordings were done during the winter 1999/2000, between the 13th of December and 17th of February.

2.2. *Test methods*

Being fed and being thwarted from access to observed food were used as positive and negative stimuli to reveal behavioural elements inferred to reflect positive and negative emotions in cattle. Access to food was used as a positive stimulus because it is generally accepted that hungry animals are pleased when they are being fed and are able to perform a motivated consummatory behaviour. The cows were starved for 7 h before they were introduced to one of the two different stimuli in a special feeding box. Half of the cows were introduced to the negative and the other half to the positive stimulus. Cows were randomly assigned to treatment groups. Cows were fed normally from the box for 2 days, five feedings in total, prior to the experiment to habituate them to the feeding box. Two exactly similar boxes were made to make it possible to record a cow exposed to one box while another was habituating to the second box. The feeding box was rectangular, made of wood and measured 0.75 m \times 0.55 m \times 0.15 m ($L \times D \times H$). The cows of the positive stimulus group were fed normally from the box. When animals that were to be thwarted were introduced to the food, the box had a top of Plexiglas with 16 holes, which were 0.7 cm in diameter. The cows could then both see and smell the food, but were not able to reach it. The box was put where the cow normally ate, and the whole meal was put in the

box in both groups. [Duncan and Wood-Gush \(1971\)](#) performed a similar experiment where food was covered by glass to frustrate adult hens.

The animals were videotaped for 6 min, starting immediately after the stimulus was introduced. The stationary camera was placed 1 m in front of the cow, approximately 1 m above floor level. As our experimental cows are used to unfamiliar persons and equipment, habituation to the camera was considered unnecessary. The videocassette recorder was a VHS Panasonic AG-6720. The camera was Panasonic CCD WV-CP 220. Behaviour was taped in colour at normal speed.

2.3. Behaviour observations

The frequencies during the 6 min test of the following behaviours were recorded by continuous sampling: vocalization, tongue rolling, aggressive behaviour, and head shaking. Vocalization was observed as a cow giving a sound, with the mouth either closed or open. Tongue rolling was recorded when the cow, in a recurrent and undeviating fashion, rolled her tongue backwards towards the region of the pharynx inside her open mouth ([Redbo, 1990](#)). Bouts were separated by the cow showing at least 1 s of another behaviour. Aggression was in this experiment defined as butting, or attempts to butt, one of the neighbours on either side of the focal cow. Recording of incidences of head shaking was included, as initial inspection of the videos showed this to be performed by several cows.

Measurements of visible eye areas were done six times during the 6 min of observation, which is every minute \pm approximately 30 s. The exact times were chosen to get acceptable views of the eye, i.e. when the cow's head was approximately perpendicular to the camera. When the cow's nose was fronting the camera it was not possible to see and make any measurements of the eyes. This also means that the eye-white was not measured at times when the cow inspected the camera. The area measures were never done in connection with blinking or during movements of the head or eyes. For the cows with access to food, the measures were frequently taken when the cow was not in direct contact with feed. The two orthogonal diameters of both the total visible eye (the sclera/cornea complex not covered by eyelids) and of the dark iris/pupil complex were measured by a ruler placed physically on the monitor when the picture was frozen. These diameters and examples of eyes in different situations are demonstrated in [Fig. 1](#). The two areas (total eye: T ; iris: I) were calculated by use of the formula for an ellipse, as an approximation of the exact areas. The percentage of white of the total visible eye area (PW) was then calculated as: $PW = 100((T - I)/T)$. Neither the intensity nor the direction of light sources was changed during the observation period.



Fig. 1. Examples of eyes varying in their percentage of the white shown. Diameters used for measurement of percentage of white in the eye are demonstrated to the right.

Control observations meant to represent a basal (neutral) percentage of white in the eye where done in the middle of the day, the same day for all cows, on the same 24 cows outside the test situation when they were standing up without showing any consummatory behaviour. One measure per individual was made.

2.4. Statistics

Statistical analysis was performed by Fisher's exact test to test for differences in the occurrence of behaviour patterns between food-rewarded and food-deprived cows (Statistical Analysis Systems Institute (SAS), 1986). Wilcoxon two-sample tests were performed to compare the percentages of eye-white in the two groups at each minute of the test. Tests on differences between time periods within groups were made by Student's *t*-test with pairwise comparisons. Frequencies of behaviour patterns in food-deprived cows were Pearson-correlated with the percentage of white of the eye. For this purpose, the average of the six measures of eye-white percentages was used for each individual. In this way, both behaviour and eye-white percentage represented the whole test period.

3. Results

The percentages of the eye-white in both groups of cows are shown in Fig. 2, in comparison with a normal control situation represented as a horizontal line. The control line represents the mean percentage of white in the eye for these 24 cows outside the test situations, being 25% (S.D. = 2.7%) with a range of 19–28%. In the test situations, the percentages of white in the eyes just before onset of stimuli (0-point) were also close to this neutral line, confirming its relevance. After onset of stimuli this percentage was decreased

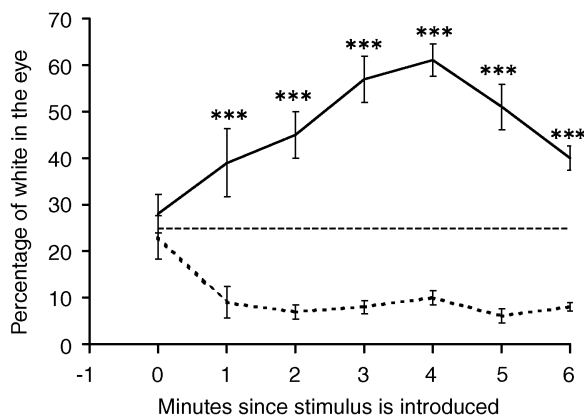


Fig. 2. The percentage of white in the eyes of fed and food deprived cows during a 6 min test (mean \pm S.E.). The dotted line represents cows given food, while the continuous line represents the food deprived cows. Each observation was done within ± 30 s of every whole minute after start of feeding or deprivation. The straight, hatched line indicates the average percentage of white in the eye in a neutral situation, i.e. when no specific stimulus is introduced to the cow. *** $P < 0.001$, Wilcoxon two-sample test.

Table 1

Distribution of observed behaviour elements among the 24 cows in the 6 min test

Behaviour	Numbers of animals showing behaviour			Frequency of behaviour in food-deprived cows Mean \pm S.E.
	Fed ($n = 12$)	Food deprived ($n = 12$)	P^a	
Vocalization	0	5	0.037	0.92 \pm 0.50
Head shaking	0	6	0.014	0.92 \pm 0.30
Tongue rolling	0	4	0.093	0.42 \pm 0.19
Aggression	0	10	0.00006	3.00 \pm 0.80

^a Fisher's exact test on the two groups.

in the animals given food, while it was increased in the food-deprived cows. There were significant differences between the two groups of cows every minute except for minute zero (Fig. 2). The percentage of white in the eyes of the food-deprived cows increased monotonously until reaching a top of about 60% after approximately 4 min and then decreased. The increase from the control condition was significant by 2 min after start ($t = 4.03$, $P = 0.002$), being exhibited by 11 of 12 cows, and was significant at each point thereafter (at 6 min: $t = 5.80$, $P = 0.0001$). The decrease from 4 to 6 min after start was observed in 10 of 12 cows ($t = 4.16$, $P = 0.002$). The percentage of white in the eyes of the fed cows decreased quickly after the stimulus was introduced and stayed on average below 10% as long as the observations were performed. The decrease was statistically significant already by 1 min after feeding (compared to control: $t = 5.00$, $P = 0.0004$; compared to 0-point: $t = 2.63$, $P = 0.023$) and for the rest of the test period. Eating was not finished during this period; the cows typically eating this amount of food for about 30 min.

None of the 12 cows given access to food from the box showed any of the observed behaviour patterns: aggression, stereotypies, head shaking, or vocalizations (Table 1). Eleven of the 12 food-deprived cows showed two or more of these behaviour patterns during the test period. Five of the 12 food-deprived animals vocalized during the 6 min of observation, the frequency of these five ranging from one to six. Four food-deprived cows performed one or two bouts of tongue rolling. Ten of the food-deprived cows showed aggression towards neighbours from one to eight times, in total 36 times. Six of the deprived cows also shook their head from one to three times during the test period.

As among the recorded behaviour patterns only aggressive butts were exhibited by a large majority of the thwarted cows, only this behaviour could be tested for correlation with the eye-white percentage. The number of aggressive butts shown by the cows was strongly correlated with their individual average percentage of white area in the eyes during the test ($r = 0.85$, $P = 0.0005$).

4. Discussion

Some of the food-deprived cows were aggressive, showed tongue rolling or head shaking, or vocalized, while these behaviour patterns were never observed among cows

given food. The present experiment supports the view that stereotypies and vocalization may be indicators of poor welfare (e.g., Broom, 1991; Weary and Fraser, 1985). The frequent observations of aggression among the food-deprived animals also support the idea that aggression may be among an animal's first reactions to uncomfortable situations. The frustration–aggression hypothesis introduced by Dollard et al. (1939) stated that aggression is always the consequence of some kind of frustration and that the occurrence of aggression always presupposes the existence of frustration. In 1941 they modified their view to state that frustration can lead to a tendency to perform a number of different types of responses, one of which is some form of aggression (Miller et al., 1941). Scott (1948) tested the effects of delayed feeding in goats to illuminate behavioural consequences of frustration. He found an increased amount of aggressive fighting in dominant animals while it caused subordinate animals to take more punishment and almost never caused aggression in them. In our cows, the dominant ones might have tried to manipulate their subdominant neighbours to get access to their food. Dominance relationships were however not assessed in the present experiment. As 10 of 12 randomly tested cows showed aggression, a high social rank could hardly explain all such incidences.

The observed head shaking in the frustrative situation, in the absence of insects, is also reported in horses (Cook, 1992). We suggest that this pattern may be a kind of displacement activity. According to the “disinhibition hypothesis” suggested to explain displacement activities, two conflicting tendencies inhibit one another and in doing so allow a third motivational system to be expressed (Van Iersel and Bol, 1958). This third motivation seems to frequently represent body care, perhaps because such motivations are frequently present but at low priority. McFarland (1965) suggested that displacement activities not only occur during a conflict between two competing motivations, but also when highly motivated behaviour is thwarted from their eliciting stimuli.

The percentage of white seen in the eyes consistently increased in the food deprived animals, and decreased in the animals given food, compared to animals not presented with any specific stimulus. The positive correlation between number of aggressive butts and percentage of white in the eye indicates that both behavioural patterns reflect the same underlying emotion. We hypothesize that showing the white of the eye, brought about by withdrawal of the eyelids, is a sign of frustration or other kind of stress reaction. In such a situation the function is probably to be able to see clearly to detect solutions to the problem. Adrenaline released by the sympathetic nervous system causes the eyes to open up more widely, as evidenced by the link to the mechanism behind pupil dilatation (Cunningham, 1997). In a human-ethology context, Ekman (1979) offered a similar explanation for the origin of the raised brows in surprise: raising the brows increases the superior visual field allowing more to be seen and more light to enter the retina. According to Ekman (1992), all members of the species might learn to use this muscular action in expressions like surprise, which metaphorically involve taking in more or unexpected input. In animals, this behaviour pattern is probably innate. We suggest that the increased percentage of white in the eye can generally be seen as an indicator of activation of a motivational system, involving the need to monitor the environment carefully. When a cow performs consummatory behaviour like eating, ruminating, drinking, or resting, the eyes are more often closed or half closed, indicating a deactivation of the motivational system. This is sometimes called a consummatory face. Feeding animals may sometimes close their eyes

to protect them from being injured or irritated by food parts. As the eye-white of the cows given access to food in our study frequently was measured when the cow was not in direct contact with food, this protective response could not explain the consistent low values observed.

Negative emotions occur when discrepancies between Istwert and Sollwert (Wiepkema, 1987) increase in magnitude or continue to exist (Bracke et al., 1999). In Wiepkema's homeostatic motivation model, incoming signals (Istwert = true value) are compared with corresponding neural configurations of the ideal state (Sollwert = ideal value). What kind of behaviour changes that occur depends on the sort of the experienced match or mismatch (Wiepkema, 1985). Not being fed when hungry is an example of such a situation, which is clearly aversive to animals. An increase in the percentage of white in the eye could therefore be an indicator of some kind of negative emotion or aversion in dairy cattle. The apparent gradual increase in the eye-white percentage during the first 4 min may indicate a gradual increase in frustration. The significance of the apparent decrease after this stage is unclear and should not be interpreted too far, but if this decrease is real we suggest that it could indicate the onset of one of several possible compensating neuroendocrine mechanisms. It is, however, a possibility that wide eyes will appear in other contexts when cows are introduced to other extreme stimuli of any kind, as an indication of a general arousal not necessarily negative in nature. Positive reward occurs in cases where discrepancies between Istwert and Sollwert are reduced or minimized (Bracke et al., 1999), as when a hungry animal is fed. We therefore, assume that the observed decrease in the percentage of the white in the eye of such animals can be linked to positive emotions related to satisfied needs.

The percentage of white in a given situation varied somewhat between individual cows. It is thus, necessary that the farmer knows each individual cow to be able to estimate the significance of a smaller decrease or increase in the white area in a practical welfare evaluation. Our interpretation of reduced percentage of eye white in cows is similar to the idea that the "blinking reaction", a marked blinking with the eyelids not to be mixed with a reflexive blinking caused by irritations in, e.g. captive lynxes may reflect how stress free and comfortable the animal "feels" (Pfleiderer and Leyhausen, 1995). Such blinking is seen in several mammals and has a social function. When a human blinks markedly to a dog or cat, the animal appears to calm down and frequently returns the signal. We suggest that this kind of blinking in animals may be an exaggerated and ritualized signal expressing the relaxedness and contentedness that is generally reflected by half-closed eyes.

Emotions evolved for their adaptive value in dealing with fundamental life-tasks (Ekman, 1992). Emotional expressions provide information to conspecifics, as well as to other animals, about antecedent events, concomitant responses, and the probable ensuing behaviour (Ekman, 1992). One possible explanation for the few positive welfare indicators known in animals is that each of the positive emotions does not have a distinctive behavioural expression (Ekman and Friesen, 1982), although each of the basic negative emotions does have such a specific behavioural expression. Perhaps it has not been relevant to survival to know which positive emotion was occurring in a flock mate, only that it was a positive emotion rather than anger, fear, disgust, or sadness (Ekman, 1992). Darwin implies this idea in his principle of antithesis, which is one of the three terms in which he suggested emotional expressions could be explained (Darwin, 1872). Behaviours of opposite kind,

e.g. aggressive and friendly behaviour and dominance and submission, are expressed in ways that are the opposite of each other. In our experiment, the wide-open eyes in frustrated cows and the half-closed eyes in the rewarded cows may reflect the same principle.

5. Conclusion

The calculated percentage of white in the eyes was larger in the food-deprived cows compared to the cows that were offered food, with a control condition providing intermediate values. Our study supports earlier reports showing that stereotypies and vocalizations are indicators of frustration and thus poor welfare. The frequency of aggressive butts correlated strongly with eye-white percentage, thus, providing validating evidence for the significance of the eye-white percentage. This behaviour element could therefore, be a dynamic indicator of emotions in dairy cattle, a high percentage indicating frustration and a low indicating satisfaction. There is, however, a need for more experiments where the cows are introduced to stimuli of different characters to clarify the generality of this relationship and to reveal to what extent small changes in the percentage of white reflect small changes along the frustration–contentedness axis. The latter would be necessary in order to elucidate whether the eye-white percentage could represent a true scale along this axis.

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References

- Baxter, M., 1983. Ethology in environmental design for animal production. *Appl. Anim. Ethol.* 9, 207–220.
- Bracke, M.B.M., Spruijt, B.M., Metz, J.H.M., 1999. Overall animal welfare assessment reviewed. *Neth. J. Agric. Sci.* 47, 279–322.
- Broom, D.M., 1983. Stereotypies as animal welfare indicators. In: Smidt, D. (Ed.), *Indicators Relevant to Farm Animal Welfare. Current Topics in Veterinary Medicine Animal Science*, Vol. 23. Nijhoff, The Hague, pp. 81–87.
- Broom, D.M., 1991. Animal welfare—concepts and measurement. *J. Anim. Sci.* 69, 4167–4175.
- Carlstead, K., 1986. Predictability of feeding: its effects on agonistic behaviour and growth in grower pigs. *Appl. Anim. Behav. Sci.* 16, 25.
- Cook, W.R., 1992. Headshaking in horses—an afterword. *Compendium on Continuing Education for the Practicing Veterinarian* 14, 1369–1371.
- Cunningham, J.G., 1997. *Textbook of Veterinary Physiology*, 2nd Edition. Saunders, New York.
- Darwin, C., 1872. *The Expression of the Emotions in Man and Animals*. University of Chicago Press, Chicago.

- Dawkins, M.S., 1980. *Animal Suffering: The Science of Animal Welfare*. Chapman & Hall, London.
- Dawkins, M.S., 1988. Behavioural deprivation: a central problem in animal welfare. *Appl. Anim. Behav. Sci.* 20, 209–225.
- Dollard, J., Doob, L.W., Miller, N.E., Mowrer, O.H., Sears, R.R., 1939. *Frustration and Aggression*, Yale University Press, New Haven.
- Duncan, I.J.H., Wood-Gush, D.G.M., 1971. Frustration and aggression in the domestic fowl. *Anim. Behav.* 19, 500–504.
- Dunn, C.S., 1990. Stress reactions of cattle undergoing ritual slaughter using two methods of restraint. *Vet. Rec.* 126, 522–525.
- Ekman, P., 1979. About brows: emotional and conversational signals. In: von Cranach, M., Foppa, K., Lepenies, W., Ploog, D. (Eds.), *Human Ethology*. Cambridge University Press, Cambridge, pp. 169–248.
- Ekman, P., 1992. An argument for basic emotions. *Cogn. Emotion* 6, 169–200.
- Ekman, P., Friesen, W.V., 1982. Felt, false and miserable smiles. *J. Nonverbal Behav.* 6, 238–252.
- Hughes, B.O. (Ed.), 1988. Discussion 3. In: *Proceedings of Workshop Sponsored by the Farm Animal Care Trust and the Universities Federation for Animal Welfare. Behavioural Needs of Farm Animals*, *Appl. Anim. Behav. Sci.* 19, 377–383.
- Jensen, M.B., Vestergaard, K.S., Krohn, C.C., 1998. Play behaviour in dairy calves kept in pens: the effect of social contact and space allowance. *Appl. Anim. Behav. Sci.* 56, 97–108.
- McFarland, D.J., 1965. On the causal and functional significance of displacement activities. *Z. Tierpsychol.* 23, 217–235.
- Miller, N.E., Sears, R.R., Mowrer, O.H., Doob, L.W., Dollard, J., 1941. The frustration–aggression hypothesis. *Psychol. Rev.* 48, 337–342.
- Nielsen, L.H., Mogensen, L., Krohn, C., Hindhede, J., Sørensen, J.T., 1997. Resting and social behaviour of dairy heifers housed in slatted floor pens with different sized bedded lying areas. *Appl. Anim. Behav. Sci.* 54, 307–316.
- Pfleiderer, M., Leyhausen, P., 1995. “Passives Abwehrsyndrom” und der Begriff des Wohlbefindens. In: *Aktuelle Arbeiten zur artgemässen Tierhaltung 1994*. KTBL Schriften, Münster Hiltrup, pp. 75–84.
- Redbo, I., 1990. Changes in duration and frequency of stereotypies and their adjoining behaviours in heifers, before, during and after the grazing period, during and after the grazing period. *Appl. Anim. Behav. Sci.* 26, 57–67.
- Samraus, H.H., 1985. Stereotypies. In: Fraser, A.F. (Ed.), *Ethology of Farm Animals*. Elsevier, New York (Chapter 3).
- Scott, J.P., 1948. Dominance and the frustration–aggression hypothesis. *Physiol. Zoöl.* 21, 31–39.
- Spruijt, B.M., van den Bos, R., Pijlman, T.A.F., 2001. A concept of welfare based on reward evaluating mechanisms in the brain: anticipatory behaviour as an indicator for the state of reward systems. *Appl. Anim. Behav. Sci.* 72, 145–171.
- Van Iersel, J.J., Bol, A.C.A., 1958. Preening in two tern species. a study of displacement activities. *Behaviour* 13, 1–88.
- Van Rooijen, J., 1984. Impoverished environment and welfare. *Appl. Anim. Behav. Sci.* 12, 3–13.
- Watts, J.M., Stookey, J.M., 2000. Vocal behaviour in cattle: the animal’s commentary on its biological processes and welfare. *Appl. Anim. Behav. Sci.* 67, 15–33.
- Weary, D.M., Fraser, D., 1985. Signaling need—costly signals and animal welfare assessment. *Appl. Anim. Behav. Sci.* 44, 159–169.
- Wiepkema, P.R., 1985. Abnormal behaviours in farm animals: ethological implications. *The Netherlands J. Zool.* 35, 279–299.
- Wiepkema, P.R., 1987. Behavioural aspects of stress. In: Wiepkema, P.R., van Adrichem, P.W.M. (Eds.), *Biology of Stress in Farm Animals: An Integrative Approach*. Current Topics in Veterinary Medicine and Animal Science, Vol. 42, Marunus Nijhoff, Dordrecht (Boston) pp. 113–133.
- Zayan, R., Duncan, I.J.H., 1987. *Cognitive Aspects of Social Behaviour in the Domestic Fowl*. Elsevier, Amsterdam.