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## ASSESSING THE IMPORTANCE OF NATURAL BEHAVIOR FOR ANIMAL WELFARE

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**ABSTRACT.** The concept of natural behavior is a key element in current Dutch policy-making on animal welfare. It emphasizes that animals need positive experiences, in addition to minimized suffering. This paper interprets the concept of natural behavior in the context of the scientific framework for welfare assessment. Natural behavior may be defined as behavior that animals have a tendency to exhibit under natural conditions, because these behaviors are pleasurable and promote biological functioning. Animal welfare is the quality of life as perceived by the animal. Animals have evolved cognitive-emotional systems (“welfare needs”) to deal with a variable environment. Animals do not only have so-called physiological needs such as the need for food, water, and thermal comfort. They also need to exercise certain natural behaviors such as rooting or nest-building in pigs, and scratching or dust-bathing in poultry. All needs must be taken into account in order to assess overall welfare. The degree of need satisfaction and frustration can be assessed from scientific information about the intensity, duration, and incidence of (welfare) performance criteria such as measurements of behavior and/or (patho)physiology. Positive welfare value relates to how animals are inclined to behave under natural conditions, in preference tests, and in consumer-demand studies. Negative welfare value relates to stress, frustration, abnormal behavior, aggression, and reduced fitness. Examples are given to illustrate how the need to perform natural behaviors can be assessed following the general principles for welfare assessment, providing a first approximation of how different natural behaviors affect animal welfare.

**KEY WORDS:** Animal welfare, assessment methodology, model, natural behavior

### 1. INTRODUCTION

Over the last decades the Dutch Ministry of Agriculture, Nature and Food Quality has attempted to improve animal welfare with legislative measures, sometimes going beyond European Community directives. The ministry now strives for a European-Union-wide level playing field, where super-legislative measures, i.e., initiatives going beyond minimal legal requirements, are being transferred to market mechanisms. This requires that stakeholders in the livestock-production chain, including producers, policy makers, consumers, and retailers, need to be involved with a shared

responsibility for improving (and monitoring) animal welfare (Bracke et al., 2005). Within this context the Dutch Ministry (LNV, 2002) proposed using the five freedoms (following e.g., Brambell, 1965; FAWC, 1992; Webster, 1995; De Jonge and Goewie, 2000). This means freedom: 1. From thirst, hunger, and malnutrition; 2. From discomfort by providing an environment suitable to their species; 3. From pain, injury, and disease; 4. From fear and distress; 5. To express natural behavior. Each freedom is considered to be essential for animal welfare. Freedoms 1–4 guarantee the absence of negative symptoms of welfare. The fifth freedom, however, promotes positive welfare and includes rooting in pigs, grazing in cattle, and scratching and dust-bathing in poultry (Wijffels, 2001).

In response to this policy statement stakeholders have requested a clarification: To what extent should farming conditions be “natural,” i.e., how should the concept of natural behavior be operationalized?

Recently, a group of 22 welfare scientists formulated the biological framework underlying welfare assessment (Anonymous, 2001), which allows developing a welfare-index system (Bracke, 2001). It has never been specified, however, how this scientific framework applies to natural behaviors.

Short of integrated weighting of animal welfare together with political, ethical, and economical considerations (cf. Röder and van den Bos, 2001), this paper will stay within the descriptive domain, trying to determine what constitutes “natural behavior” and how it affects animal welfare, defined as what matters to animals from their point of view (Bracke et al., 1999a). It aims to propose a methodology for assessing the relative importance of different natural behaviors for welfare on a scientific basis.

## 2. TOWARDS A DEFINITION

A definition of natural behavior must be functional for welfare assessment. This implies, firstly, that to avoid communication problems it must be in accordance with common usage of the terms “natural” and “behavior.” Secondly, “natural behavior” should indicate positive welfare, in line with the fifth freedom, and, finally and as a general rule, the more natural the behavior the better the animal’s welfare should be. In relation to these requirements, problems associated with simple definitions of “natural behavior” will be identified, and a compound definition will be proposed. Simple definitions include behaviors that are species-specific, shown in nature, internally motivated, and pleasurable.

Behaviors such as rooting in pigs, dust-bathing in poultry, and grazing in cattle are examples of so-called species-specific behaviors, i.e., behaviors that are more or less typical of the species. Defining “natural behavior”

in terms of *species-specific* behaviors fits common usage, but, although functional for taxonomic purposes, it is not functional for welfare assessment. Some behaviors, such as play, walking, stretching limbs, turning around, and getting up and lying down normally, are common across species (so not species-specific), but nevertheless highly beneficial for welfare. In fact, several of these examples were used in the original formulation of the five freedoms (Brambell, 1965) and are widely recognized as important for animal welfare. Other behaviors, such as stereotypies and tail biting in pigs, feather pecking in poultry, and tongue rolling in calves, are highly species-specific, but indicative of reduced welfare. Defining “natural behavior” in terms of species-specific behaviors, therefore, is not functional for welfare assessment.

Secondly, the term “natural” may be interpreted as *behavior shown in nature as opposed to shown in “artificial” or “high-tech” environments*. In accordance with common usage (the first requirement), welfare concerns about intensive farming have been related to the high-tech environments that are very different from the animals’ natural environment. However, not all unnatural conditions are indicative of reduced welfare. Televisions, airplanes, and computers involve “unnatural” human activities that may nevertheless contribute positively to welfare. In animals, this may be true for milking robots (e.g., Hopster et al., 2002), and automated feeders. Conversely, certain behaviors that may occur in nature, such as predator avoidance, coping with extreme weather conditions, aggression, and sickness behavior, probably indicate reduced welfare. This definition of “natural behavior,” therefore, also fails to meet the second and third requirement (positive for welfare; the more the better).

Thirdly, “natural behavior” may be defined as behavior that is *intrinsically motivated* (cf. Hughes and Duncan, 1988). Examples include nest-building in sows (cf. Jensen, 1993) and dust-bathing in hens. These behaviors are largely controlled by internal physiology, e.g., hormones. Other behaviors such as agonistic behavior, flight, and thermoregulatory behaviors are largely externally motivated, i.e., they have to be “triggered” by external stimulation. However, as Jensen and Toates (1993) pointed out, what matters for welfare is not whether a behavior is internally motivated, but whether the (behavioral) need gets frustrated or satisfied. This argument implies that a definition in terms of internal motivation is not optimally functional for welfare.

“Natural behavior,” finally, may more widely refer to *behavior that is performed, because it is pleasurable*, in that the animals are positively motivated to perform the behavior. When the performance of a behavior itself is rewarding it is called an ethological need (which by definition is internally motivated). This definition of natural behavior excludes nega-

tively motivated behaviors such as sickness behavior and fear, and it excludes non-motivated, reflex-like behaviors, because they are not pleasurable. For humans, watching television, playing computer games, and even drug addiction are presumably pleasurable. However, these behaviors are not commonly regarded as natural behaviors and this poses a conflict with the first requirement (common usage).

The problems with simple definitions of natural behavior lead us to propose a compound definition. Adopting the three elements in animal welfare (feelings, biological functioning, and natural living) as identified by Fraser et al. (1997), the animal's nature can be regarded as having evolved sentience in a natural environment. This results in the following proposal for a compound working-definition of "natural behavior": *Natural behavior is behavior that animals tend to perform under natural conditions, because it is pleasurable and promotes biological functioning.* More precisely, natural behavior is behavior that animals have a tendency to perform when given the opportunity under (a wide range of "ad libitum") natural conditions, because the behavior is presumably pleasurable (i.e., positively motivated) and promotes biological functioning in the environment of evolutionary adaptation (i.e., the environment in which the animal evolved). This definition includes both internally and externally motivated behaviors, as long as they are positively motivated. Furthermore, the definition includes both short-term consequences (being pleasurable now) and long-term consequences (promoting biological functioning and "pleasure" at a later point in time). The compound definition applies to a wide range of behaviors such as play, searching for food, feeding, mating, locomotion, nest-building, resting, and grooming. The definition excludes sickness behavior, flight, and aggression, because (and in as far as) they are not pleasurable.

The definition was formulated to be functional for welfare assessment, but the second and third requirements (positive for welfare; the more the better) were given priority over the first (of being in accordance with common usage). Some behaviors, such as behaviors controlled by electronic equipment (milking robot, automated feeding), appear "unnatural," but they may be natural according to the proposed definition, namely when they are positively motivated and when the animals would have a tendency to perform these behaviors under more "ad libitum" (natural) conditions. If so, these behaviors can be regarded as adaptations to the (domestic) environment of evolutionary adaptation. Remaining conflicts between the component terms in the definition ("natural conditions," "biological functioning," and "pleasurable feelings") can be resolved when it is realized that these terms are continuous variables. Accordingly, the more a natural behavior is in accordance with each of the components, the more it meets the definition.

### 3. SCIENTIFIC FRAMEWORK

This section further refines a prevalent scientific conceptual framework for welfare assessment (Anonymous, 2001; Bracke et al., 2002).

Welfare, defined as an animal's quality of life, is a function of the animal's welfare needs. Animals are organisms that have evolved in the course of evolution to deal with a variable environment (Wiepkema, 1987). In order to survive and reproduce in their environment of evolutionary adaptation, which for the domesticated animals is still largely determined by their original natural environment, animals have developed a set of motivational systems, also called cognitive-emotional systems. Examples include food, water, rest, thermal comfort, body care, social contact, health (sickness behavior), exploration, and safety (see Bracke et al., 1999b). Welfare needs reflect the states of these control systems (cf. the Istwert–Sollwert model, Figure 1 modified after Wiepkema, 1987) in which animals perceive what is the case (Istwerte) and compare this with what they want (Sollwerte). A perceived mismatch between what is, and what is wanted, results in the activation of behavioral and/or physiological responses (also called animal-based performance criteria), which in the course of evolution have been designed to help resolve the mismatch. Three levels of “defense” can be distinguished, primary, secondary, and tertiary responses, which (by and large) correspond to the degree to which welfare is affected (Jaap Koolhaas,

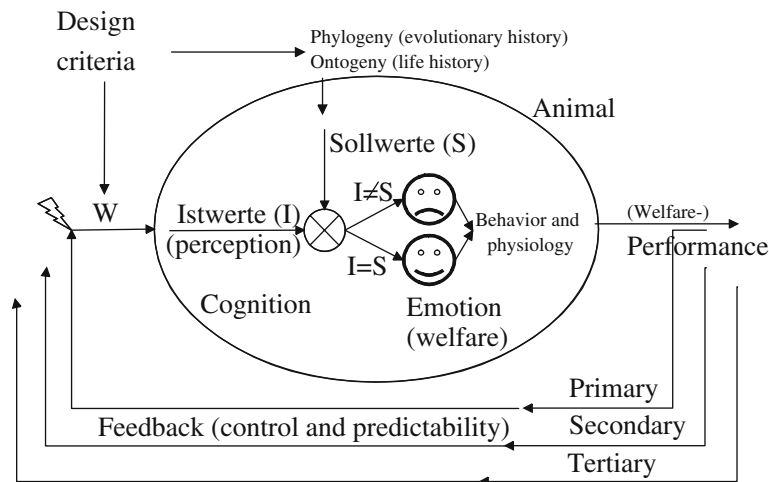


Figure 1. Conceptual framework for scientific assessment of animal welfare (see text). The actual values of the external world (W) are perceived by the animals as Istwerte (I). Emotions result from perceived (mis)matches between Istwerte and Sollwerte, leading to a cascade of (primary, secondary, tertiary) responses, which vary in functionality.

personal communication; Figure 1). Primary responses usually result in a rapid restoration of the equilibrium (homeostasis). When primary responses fail, secondary responses, e.g., stereotypic behavior and pre-pathological states, may apparently maintain homeostasis by a more or less temporary change of setpoints and norms in response to stress (so-called “allostasis,” meaning “achieving stability through change”), which may be functional on the short- and mid-term. However, on the long-term these responses may represent a risk by its wear and tear effects (so called “allostatic load”; e.g., McEwen 2002). For example, persistent stress may maintain a high blood pressure, which is a risk factor for heart disease. Tertiary responses are pathological states indicative of severe malfunction.

The Istwert–Sollwert model implies that persistent failure to reduce perceived mismatches result in stress and negative emotions, reflecting the fact that a welfare need has been frustrated. Strong frustration arises when, despite all efforts and for long periods of time, the animal does not succeed in reducing the mismatch. Conversely, a need is satisfied when the animal perceives a match between what is and what is wanted. Need satisfaction is especially strong when the animal succeeds in reducing an existing substantial mismatch with effective responses.

Sollwerte are the product of both the individual’s life history and its evolutionary history. The life history includes prenatal, ontogenetic, and learning experiences. Evolutionary history has resulted in animals that would respond in a “fit”/adapted way to most challenges in the so-called Environment of Evolutionary Adaptation (EEA). Domestication covers only a fraction of the animal’s evolutionary history and, accordingly, only marginally determines its welfare needs.

In a classic paper, Breland and Breland (1961), trained thousands of animals from a wide variety of species (including raccoons, pigs, and chickens) and reported that animals have a marked tendency to perform certain appetitive elements of feeding behavior, even when this prevented the animals from obtaining food rewards. Later studies have shown that animals will work for commodities even under ad libitum conditions. For example, hens will work for obtaining food even when this food is available ad libitum (Lindqvist and Jensen, 2003), and sows will build nests in the presence of (apparently appropriate) nests. It is now widely recognized that animals have ethological needs (Toates, 1995). These needs are controlled by the performance of the behavior, rather than by the functional (physiological) consequences, presumably because this behavior improved biological functioning in the EEA (Fraser and Duncan, 1998; Spruijt et al., 2001).

In order to assess welfare, we must determine how much each of the animal’s welfare needs have been satisfied and/or frustrated, i.e., how much animals are motivated to obtain their goals, including their motivation to

perform specific behaviors. The most direct way to learn about animal motivation is to measure the amount of work animals would be willing to perform to obtain resources (Dawkins, 1990). Information from such so-called consumer demand studies must be supplemented with other welfare measures. Welfare-relevant information describes relationships between so-called design criteria and performance criteria (Anonymous, 2001).

Design criteria are mostly environment-related “input” parameters that (causally) affect welfare. Design criteria refer mainly to “Istwerte,” but may also refer to the animal’s Sollwerte/norms. Performance criteria are mainly animal-based “output” parameters measuring the degree of activation of an animal’s behavioral and physiological responses. In addition to consumer demand studies, positive welfare performance measures include behavior observed in natural environments and preferences tests. Negative welfare indicators include symptoms of physiological stress, behavioral frustration (and aversion), aggression, abnormal behaviors, reduced health, and reduced fitness (see Bracke et al., 2002). Although each of these measures has its methodological problems (e.g., Rushen, 1991), in general, the level of biological functioning as expressed with these measures is commonly believed to indicate animal welfare.

The study of natural behavior provides welfare-relevant information, because it may be regarded as a kind of (large-scale) preference test in a rich, natural environment. For example, pigs are social animals, because whenever they get the opportunity (as in (semi)natural environments), they organize themselves in social groups (Stolba and Wood-Gush, 1989). Furthermore, most animals spend a substantial portion of their active time searching for food under natural conditions. To determine the importance of food searching, we need to know what happens with and without abundant food and/or foraging opportunities. Without food an animal dies. With abundant food, perhaps surprisingly, animals are still motivated to search for food (e.g., Singh, 1970). Food and foraging, therefore, can be identified as separate needs with different importance (as the animal does not die from a deprivation of foraging behavior). Further scientific information, e.g., about how much animals are prepared to work for food and foraging substrate (Matthews and Ladewig, 1994), may be used to determine more accurately how important these behaviors are. This illustrates how various pieces of information about welfare performance criteria can be used to assess the welfare relevance of a natural behavior. More generally, an assessment of welfare always relies on information about the relationship between design criteria and performance criteria, and often requires an integration of different performance criteria representing different aspects of biological functioning and (the correlated) underlying motivation. This implies that the assessment be made in terms of the dimensions of intensity,

duration, and incidence (after Willeberg, 1991; Anonymous, 2001). For example, the “amount” of pain is a function of its intensity, duration, and incidence. Straightforward recordings of time, frequencies, and numbers of affected animals suffice to determine the dimensions of “duration” and “incidence.” “Intensity” may be more difficult to quantify. It refers to the level of (positive or negative) “demand” (for, in this case, pain avoidance).

#### 4. SOME NATURAL BEHAVIORS WEIGHTED FOR WELFARE

Table 1 shows a tentative example of how the importance of several natural behaviors in different species housed in conventional housing systems may be assessed relative to each other. The behaviors are scratching in poultry, rooting in pigs, social contact for sows and boars, grazing and natural breeding in dairy cattle, and the weaning of calves and piglets as perceived by the mother. A tentative order of importance as determined on the basis of an exemplary assessment of the intensity, duration, and incidence of the behaviors and their consequences led to the following ranking (from 1, most important, to 5, least important): 1: poultry, rooting in pigs, 2: social contact for sows, 3: grazing for dairy cattle, 4: social contact for boars, 5: natural breeding in dairy cattle, and the weaning of calves and piglets as perceived by the mother. To finalize this ranking, a more detailed analysis and literature study would be required. A first step towards this was made, but this part of the text had to be cut in order for this text to fit into the special issue of the journal. However, for the present purposes the table may serve as an example of how the assessment may be performed.

### CONCLUSIONS

The aims of this paper were to define the concept of “natural behavior” and to formulate principles for assessing the welfare importance of different natural behaviors. We defined natural behavior as behavior that animals have a tendency to perform under natural conditions because these behaviors are pleasurable and because they promote biological functioning. It includes behaviors such as foraging, grooming, exploration, and play. It excludes negatively motivated behaviors such as fear responses and abnormal behaviors.

The scientific framework for welfare assessment regards animals as having cognitive-emotional control systems that have evolved in the course of evolution to deal with a variable environment. The framework allows for the formulation of general rules for welfare assessment. These rules also apply to the assessment of (the importance of) natural behaviors. Natural



Table 1. Assessments of the importance of several natural behaviors.

	Scratching in poultry	Rooting in pigs	Social contact for sows	Grazing in dairy cattle	Social contact for boars	Natural breeding in dairy cattle	Weaning of calves and piglets as perceived by the mother
Intensity	(Very) High	(Very) High	High	Moderate	Moderate	Moderate	Moderate
Duration	(Very) Long	(Very) Long	(Very) Long	(Very) Long	(Very) Long	Short (days)	Short (days)
Incidence	High	High	High	High	High	Low (1-2/year)	Low (1/year)
Istwert-Sollwert discrepancy in the housing system	Large (in battery cages)	Large (in straw less systems)	Large (in individual housing)	Large (without pasture)	Small (solitary animals)	Moderately high?	Moderately high?
Biological significance	High	High	Rather high	High	Low	Moderate	Moderate
Negative welfare symptoms	Feather pecking	Tail biting, stereotypies	Actuate Isolation stress and abn. behav.?	No abn. behav., lameness	None	Some restlessness	Some restlessness
Subjective assessment	Very important	Very important	Important	Rather important	Moderately important	Relatively unimportant	Relatively unimportant

Abn. behav: abnormal behavior. Note that the classification of “rather important” for grazing in dairy cattle is higher than “moderately important” for social contact of boars, but probably not “significantly different” (due to a relatively large error margin for this tentative table).

behaviors are welfare performance criteria, which are animal-based indicators of welfare. Welfare performance criteria such as natural behaviors, preferences, demand, stress and (other) measures of biological functioning, can be weighted in terms of their intensity, duration, and incidence, where the ultimate criterion is the degree of motivation these measures represent.

The following steps involved in the operationalization of natural behaviors can be identified:

1. Specify the natural behavior that is to be assessed.
2. Identify the requirements for performing the behavior.
3. Identify all consequences of (not) being able to perform the behavior.
4. Quantify the intensity, duration, and incidence of the underlying motivation, thus assessing the scope of the welfare need.
5. Determine the degree to which the natural behavior can be performed in the housing system under assessment.
6. Identify to what extent the housing system is thus meeting the animal's need to express that behavior.

For the purpose of ethical and political decision making and the ultimate operationalization of natural behavior, the welfare importance must be weighted with other animal and human interests. Cut-off points may have to be determined for what we humans find acceptable. The ethical and political assessments often require that a method for the welfare assessment of natural behavior is available and that actual assessments have been made. This paper intended to deliver such a method and presented a preliminary priority list of several natural behaviors for different farm animals. Although it appears to be a comparison of apples and oranges, the proposed method allowed a comparison across species. This is because for welfare it is not relevant which individual experiences the emotions/feelings. What counts is the degree of need satisfaction and/or need frustration. In our example, foraging behavior and social contact (excluding aggression) were the most important behaviors, especially because of the high incidence and duration of these daily behaviors compared to the less frequently performed behaviors related to the reproductive cycle. Under present husbandry conditions, foraging of pigs (rooting) and poultry (scratching) were the most important, e.g., when compared to grazing of dairy cattle, because deprivation of grazing does not lead to abnormal behaviors. Foraging is, therefore, not only important because it is performed under natural conditions, but also because of the consequences for biological functioning, including the amount of work the animals are prepared to deliver in order to be able to perform the behavior.

The methodology suggested in this paper can be used to determine priorities for natural behaviors in a more detailed and definitive way. The

concept of natural behavior, as specified in this paper, however, does not only indicate points of attention for further scientific research (e.g., on natural behavior and formalized assessment), it also promises to be a useful concept to help tackle persistent welfare problems in present-day industrialized societies.

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#### REFERENCES

- Anonymous (2001), "Scientists' Assessment of the Impact of Housing and Management on Animal Welfare," *Journal of Applied Animal Welfare Science* 4, pp. 1–52.
- Bracke, M. B. M., K. H. de Greef, and H. Hopster (2005), "Qualitative Stakeholder Analysis for the Development of Sustainable Monitoring Systems for Farm Animal Welfare," *Journal of Agricultural and Environmental Ethics* 18(1), pp. 27–56.
- Bracke, M. B. M., B. M. Spruijt, and J. H. M. Metz (1999a), "Overall Welfare Assessment Reviewed. Part 1: Is it Possible?," *Netherlands Journal of Agricultural Science* 47, pp. 279–291.
- Bracke, M. B. M., B. M. Spruijt, and J. H. M. Metz (1999b), "Overall Animal Welfare Reviewed Part 3: Welfare Assessment Based on Needs and Supported by Expert Opinion," *Netherlands Journal of Agricultural Science* 47, pp. 307–322.
- Bracke, M. B. M. (2001), *Modelling of Animal Welfare: The Development of a Decision Support System to Assess the Welfare Status of Pregnant Sows*, PhD dissertation, Wageningen.
- Bracke, M. B. M., B. M. Spruijt, J. H. M. Metz, and W. G. P. Schouten (2002), "Decision Support System for Overall Welfare Assessment in Pregnant Sows A: Model Structure and Weighting Procedure," *Journal of Animal Science* 8, pp. 1819–1834.
- Brambell, R. W. R. (1965), *Report of the Technical Committee to Enquire into the Welfare of Livestock Kept in der Intensive Husbandry Conditions*, Cmnd 28, HMSO, London.
- Breland, K. and M. Breland (1961), "The Misbehavior of Organisms," *American Journal of Psychology* 16, pp. 681–684.
- Dawkins, M. S. (1990), "From an Animal's Point of View: Motivation, Fitness, and Animal Welfare," *Behavior and Brain Science* 13, pp. 1–61.
- FAWC (Farm Animal Welfare Council) (1992), "FAWC Updates the Five Freedoms," *Veterinary Record* 131, p. 357.

- Fraser, D., D. M. Weary, E. A. Pajor, and B. N. Milligan (1997), "A Scientific Conception of Animal Welfare that Reflects Ethical Concerns," *Animal Welfare* 6, pp. 187–205.
- Fraser, D. and I. J. H. Duncan (1998), "'Pleasures', 'Pains' and Animal Welfare: Toward a Natural History of Affect," *Animal Welfare* 7, pp. 383–396.
- Hopster, H., R. M. Bruckmaier, J. T. N. van der Werf, S. M. Korte, J. Macuhova, G. Korte-Bouws, and C. G. Reenen (2002), "Stress Responses During Milking: Comparing Conventional and Automatic Milking in Primiparous Dairy Cows," *Journal of Dairy Science* 85, pp. 3206–3216.
- Hughes, B. O. and I. J. H. Duncan (1988), "The Notion of Ethological 'Need', Models of Motivation, and Animal Welfare," *Animal Behaviour* 36, pp. 1696–1707.
- Jensen, P. (1993), "Nestbuilding in Domestic Sows: The Role of External Stimuli," *Animal Behaviour* 45, pp. 351–358.
- Jensen, P. and F. M. Toates (1993), "Who Needs Behavioural Needs – Motivational Aspects of the Needs of Animals," *Applied Animal Behaviour Science* 37, pp. 161–181.
- De Jonge, F. H. and G. A. Goewie (2000), *In het Belang van het Dier: Over het Welzijn van Dieren in de Veehouderij [In the interest of the Animal: About the Welfare of Animals in Livestock Production]*, The Hague: Rathenau Institute.
- Lindqvist, C. and P. Jensen (2003), "Contra Freeloading Decreases with Age and Social Isolation in Red Jungle Fowl and White Leghorn Layers," in V. Ferrante (ed.), *Proceedings of the 37th International Congress of the ISAE*, Fondazione Iniziative Zooprofilattiche e Zootecniche, Brescia, p. 159.
- LNV (2002). Beleidsnota Dierenwelzijn, Maart 2002 (Animal Welfare Policy Memorandum, March 2002). The Hague: LNV.
- McEwen, B. S. (2002), "Sex, Stress and the Hippocampus: Allostasis, Allostatic Load and the Aging Process," *Neurobiology of Aging* 23, pp. 921–939.
- Matthews, L. R. and J. Ladewig (1994), "Environmental Requirements of Pigs Measured by Behavioural Demand Functions," *Animal Behaviour* 47, pp. 713–719.
- Röder, E. and R. van den Bos (2001), *Passen en meten? Over soorteigen gedrag en dierenhuisvestingsbeleid bij productiedieren, proefdieren en plezierdieren [Fitting and Measuring About Species-Specific Behaviour and Policy Making on Housing for Livestock, Laboratory Animals and Pets]*, The Hague: NWO Ethiek & Beleid.
- Rushen, J. (1991), "Problems Associated with the Interpretation of Physiological Data in the Assessment of Animal Welfare," *Applied Animal Behaviour Science* 28, pp. 381–386.
- Singh, D. (1970), "Preference for Bar Pressing to Obtain Reward Over Freeloading in Rats and Children," *Journal of Comparative Physiological Psychology* 73, pp. 320–327.
- Spruijt, B. M., R. Bos, and F. T. A. Pijlman (2001), "A Concept of Welfare Based on Reward Evaluating Mechanisms in the Brain: Anticipatory Behaviour as an Indicator for the State of Reward Systems," *Applied Animal Behaviour Science* 72, pp. 145–171.
- Stolba, A. and D. G. M. Wood-Gush (1989), "The Behaviour of Pigs in a Semi-natural Environment," *Animal Production* 48, pp. 419–425.
- Toates, F. M. (1995), *Stress: Conceptual and Biological Aspects*, Chichester: Wiley.
- Webster, J. (1995), *Animal Welfare: A Cool Eye Towards Eden*, Oxford: Blackwell.

- Wiepkema, P. R. (1987), "Behavioural Aspects of Stress," in P. R. Wiepkema and P. W. M. van Adrichem (eds.), *Biology of Stress in Farm Animals: An Integrative Approach*, Dordrecht: Martinus Nijhoff, pp. 113–133.
- Wijffels (2001), *Toekomst voor de veehouderij. Agenda voor een herontwerp van de sector [Future for Livestock Production. Agenda for a Redesign of the Sector]*, Report of the Commission Wijffels, The Hague.
- Willeberg, P. (1991), "Animal Welfare Studies: Epidemiological Considerations," *Proceedings of the Society for Veterinary Epidemiology and Preventive Medicine*, London, pp. 76–82.

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