



From the individual to the population – and back again? Emphasising the role of the individual in animal welfare science



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ABSTRACT

During the past decades, the study of “animal personalities” has gained increasing importance in the field of behavioural and evolutionary ecology, thereby contributing to a focus shift from the population to the individual in various research disciplines. Against this background, the overall idea of the present review is to transfer the personality concept from behavioural ecology to animal welfare science, to discuss the role of the individual in different research approaches and to pave new grounds for a more individual-tailored assessment and treatment of welfare-related problems. Moreover, we will explicitly refer to welfare issues “beyond the average”, thereby addressing problems that are not entirely covered by simply studying personality traits in animal welfare research. By combining two different fields, we hope to stimulate more theoretical and empirical work on this topic to find new ways of improving the welfare of animals in human hands even at the individual level.

1. Introduction

During the past decades, the study of “animal personalities” has revolutionised the field of behavioural and evolutionary ecology, contributing to a focus shift from the population to the individual (e.g., Gosling, 2001; Réale et al., 2010, 2007). Central to this development was the accumulating evidence that behaviour is much less flexible than previously thought and that individuals of the same species differ consistently from each other concerning their behavioural and physiological patterns. Despite this increasing interest in the animal personality concept, however, there is still a great deal of uncertainty and debate about how to best conceptualise it (e.g., Zeigler-Hill and Highfill, 2017).

In animal welfare science, much effort has been put into the identification and modification of factors and conditions that influence the welfare of animals either negatively or positively. Thereby, most experimental approaches rely on group comparisons to study which causal factors lead to which effects, neglecting inter-individual differences in response patterns widely (Fraser, 2009). Since at the same time, most animal welfare scientists agree that welfare is about the individual animal (Broom, 2008), the explicit consideration of unique features of individuals may also advance our knowledge in animal welfare science. This becomes particularly evident when thinking about the work done by Jane Goodall, Dian Fossey, or other early

primatologists working in the natural habitat of their study species, who contributed much to our current understanding of social relationships and emotional states in animals by collecting detailed data of individual animals. The aim of the present review is therefore to transfer current insights from behavioural ecology to animal welfare science, to discuss the role of the individual in different research approaches and to pave new grounds for an individual-tailored assessment and treatment of welfare-related problems. The review will start by giving a brief overview of the personality concept in behavioural ecology, some historical developments in animal welfare science, and the *status quo* of research linking the two disciplines. In particular, we will discuss in a first part the existence of personality-dependent welfare problems and its consequences for (1) the design of the environment and (2) the selection of individuals that can be housed in captivity without developing welfare problems. In the second part of this review, we will then explicitly refer to welfare issues “beyond the average”, thereby addressing problems that are not entirely covered by simply studying personality traits in animal welfare research. In this respect, we will emphasise the role of the individual animal for (1) the objective assessment of welfare and (2) the treatment of welfare-related problems of animals in captivity.

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2. From the population to the individual – the concept of animal personality in behavioural ecology

Although the fact that individuals vary lies at the very centre of Darwinian evolution, the systematic study of personalities in nonhuman animals (= “animal personalities”) dates back no longer than the end of the 20th century. Since then, behavioural ecologists have started to investigate differences between individuals that had been interpreted as “non-meaningful” and “non-adaptive” variation or “noise” before. In addition to simply comparing population or group means, the individual itself had suddenly become the key target of research approaches (Weiss, 2018).

Historically, the term “personality” has been derived from human psychological research to highlight the fact that individuals of various nonhuman species do differ as consistently in behavioural traits as humans do. The term, however, is not meant to imply homology between human and nonhuman personality concepts (for a discussion of the term please see Briffa and Weiss, 2010). Over the past decade, considerable efforts have therefore been made to work out a proper definition and determine what is covered by “personality” in a non-human context (Briffa and Weiss, 2010; Réale et al., 2007). While there is still no consensus about terms and definitions, most behavioural ecologists have agreed upon the idea of personality describing inter-individual behavioural differences that are consistent over time and/or across contexts or situations (Réale et al., 2007; Wolf and Weissing, 2012). The term “consistent” thereby does not mean that trait values cannot change with age or environmental conditions, but that differences between individuals are largely maintained (Réale et al., 2007). More precisely, such a personality definition implies that an individual that tends to score higher on a particular behavioural axis at a given time as compared to its groupmates also tends to score higher on that axis at later time points, and that an individual that tends to behave more aggressively in a context A also does so in a context B (Wolf and Weissing, 2012). Thus, despite carrying a certain meaning and being prone to anthropomorphic interpretations (Briffa and Weiss, 2010), clear criteria have to be met in order to talk about animal personality in a scientific way.

Meanwhile, such consistent inter-individual differences have been described for numerous taxa, including various mammalian, bird, fish, reptile, amphibian, and even insect species (e.g., Hollander et al., 2008; Toms et al., 2010; Tremmel and Müller, 2013). Thereby, much effort has been put into identifying different personality traits or dimensions, such as boldness, activity, playfulness, or sociability (for review see Gosling, 2001; Réale et al., 2007). One of the most frequently described dimensions of behavioural variation is the shy-bold continuum (Wilson et al., 1994, 1993). It refers to an individual’s reaction to risky situations with the boldest individuals taking the most risks and the shyest ones avoiding them. Similarly, early studies by Koolhaas et al. identified time- and context- consistent inter-individual differences in so-called “coping styles” (Benus et al., 1991; Koolhaas et al., 1999). With the aim of classifying differences in responses to stress, two alternative coping styles have been identified, a “proactive” and a “reactive” one. Although this coping concept originally derived from studies on stress physiology in laboratory rats and mice, it has been transferred to various other vertebrate species, including farm animals (Koolhaas and Van Renen, 2016), and integrated in modern personality research, mainly because the two alternative coping strategies are thought to correspond to basic personality types (Caramaschi et al., 2013). Briefly, a proactive type has been linked to an enhanced sympathetic response to a stressor and a reactive type to an enhanced parasympathetic activation and a higher HPA-axis reactivity (Koolhaas et al., 1999; Caramaschi et al., 2013). More recent research indicates, however, that the relationship between aspects of coping style and neuroendocrine mechanisms is not as clear as originally thought (Koolhaas et al., 2010). On the behavioural level, a proactive individual has been found to display high levels of aggression and routine formation and low levels

of behavioural flexibility, whereas a reactive individual has been shown to exhibit low levels of aggression and routine formation and high levels of behavioural flexibility (Caramaschi et al., 2013; Koolhaas et al., 1999). Moreover, different behavioural responses between proactive and reactive animals can be observed in tests that allow animals to freely choose between two equally adaptive behavioural patterns, such as the defensive burying test or the forced swim test. These experiments particularly support the view that proactive individuals typically display high levels of offensive behaviour (e.g. by defensive burying in the defensive burying test or active swimming and struggling in the forced swim test), while reactive individuals respond in a more defensive way in these situations (e.g. by showing immobility and passively avoiding the electrified probe in the defensive burying test and showing floating behaviour in the forced swim test; Koolhaas et al., 2010).

Thus, most of the early work on animal personality has concentrated on the description of this phenomenon across taxa and on the identification of underlying neuroendocrine mechanisms, while recent attention in the field has turned to other topics, such as the study of ecological correlates and the functional significance and evolution of this phenomenon (Stamps and Groothuis, 2010a,b). From an evolutionary perspective, the emergence of such time- and context-consistent inter-individual differences is of particular interest, as a more flexible structure of behaviour is believed to provide selective advantages in rapidly changing environments. Likewise, more and more practical implications have been discussed that highlight the relevance of the concept for related research areas, including biomedical research or human psychology (e.g., Cavigelli, 2005). In this context, it has also been suggested that knowledge about consistent inter-individual differences in specific disease- or stress-related traits may have far-reaching implications for animal welfare (e.g., Carere and Maestripieri, 2013; Huntingford and Adams, 2005) or conservation efforts (e.g., Powell and Gartner, 2011; Smith and Blumstein, 2013; Watters and Powell, 2012). For example, it has been argued that in a domestic context variation in the way individuals respond to environmental challenges or experimental treatments may have important consequences for health and/or disease development (Koolhaas and Van Renen, 2016). Therefore, as animal welfare scientists, what can we learn from behavioural ecology? Do we need to better integrate the concept of animal personality in modern animal welfare science and shift our focus from the population to the individual?

3. A short walk through the history of animal welfare science

Whereas most scientific disciplines have emerged from curiosity or practical motivations of their pioneers, modern animal welfare science started to develop as a response to the changing attitude of humans towards animals (Fraser, 2008). These ethical concerns of society about how animals are housed and treated were particularly elicited by the book “Animal Machines”, in which the British animal welfare activist and author Ruth Harrison described the conditions of farm animals, mainly laying hens, sows and veal calves, in confined production systems (Harrison, 1964). As a reaction to this seminal book and the subsequent heightened public concern for farm animal welfare, the UK government established first the Brambell Committee (Brambell, 1965) and later the Farm Animal Welfare Council who formalised the “Five Freedoms” for “animals kept under intensive livestock husbandry systems” (FAWC, 2009). The Five Freedoms consist of the freedom from hunger and thirst, from discomfort, from pain, injury or disease, from fear and distress, and the freedom to express normal behaviour, and still form the basis for animal welfare research to date (e.g., in the EU-funded project WelfareQuality®, Blokhuis et al., 2010). Even though specifically formulated for farm animals, the principles of the Five Freedoms have been transferred to all animals under human care over recent years, including companion (e.g., Rochlitz, 2005), laboratory (e.g., Morton and Hau, 2002) and zoo animals (e.g., Scott et al., 2000). Since the formulation of the Five Freedoms, however, both research foci

and methodological approaches in animal welfare science have further developed and changed (Mench, 1998). Originally, animal welfare science has focused on reducing suffering in animals, for example resulting from injuries, pain or severe stress (e.g., Morton and Griffiths, 1985; Weary et al., 2006). This has changed at the end of the last century, when the assessment and promotion of positive welfare started to gain more and more attention (e.g., Boissy et al., 2007; Mench, 1998; Yeates and Main, 2008) aiming at a “life worth living” or preferably “a good life” for animals (FAWC, 2009). Likewise, the methodologies developed and applied to assess animal welfare have undergone a drastic change from a former focus on health and functioning towards the integration of the animals’ perspective, including the study of animal emotion (Lawrence, 2008; Mench, 1998). Even though animal welfare scientists might differ in how they weigh the importance of the different methodological approaches, most of them seem to agree that animal welfare includes both aspects of physical health and emotional well-being (e.g., Broom, 2011; Dawkins, 2004). Moreover and most interestingly with respect to the focus of this review, it is consensus that animal welfare is about the individual animal, considering the “individual variation in attempts to cope with adversity and in the effects which adversity has on the animal” (Broom, 2008, p. 86). If the aim is therefore to avoid suffering in all animals of a group, we need to be concerned about each of the individuals within this group – a concern of recent discussion, especially when assessing the welfare of animals living in large groups (Winckler, 2018).

Despite this agreement on the relevance of the individual, most of the work focuses on populations or groups rather than the individual animal. Classically, groups of animals experiencing different treatments, for example, by being housed in either condition A or condition B, are compared with each other to study treatment-dependent effects on the welfare of the animals. Outcome measures include health and production parameters (e.g., Cozzi et al., 2005) as well as behavioural (e.g., measures of anxiety-like behaviour or activity, Lukkes et al., 2009), physiological (e.g., concentrations of stress hormones, Ramsay et al., 2006), and/or cognitive measures (e.g., judgement biases, Bateson and Matheson, 2007). Usually, such studies focus on commonalities across individuals, thereby largely neglecting inter-individual variation. This tendency is also mirrored in how statistics are taught and applied in the field: Most approaches are based on measures of central tendency (mean, median) that allow for testing hypotheses or drawing more general conclusions about the groups the animals belong to (Fraser, 2009). However, ensuing from the increasing interest in the concept of animal personality and the concern for each individual’s welfare state, personality measures have started to be integrated into animal welfare research as a tool to emphasise the role of the individual animal.

4. Part I - the study of animal personality in animal welfare research

In the past decades, a variety of behavioural tests to identify different personality traits, such as fearfulness or boldness, has been developed and applied in animal welfare science, shedding light on the complex relationship between animal personality and animal welfare. In particular, the aim of these developments has been to investigate if and how certain personality traits may affect or interact with specific welfare measures. In fish kept in high densities, for example, it has been shown that the personality traits aggressiveness and risk-taking have an immediate effect on fish welfare with non-aggressive individuals that avoid risks gaining less food and growing more poorly than their more aggressive conspecifics (Huntingford and Adams, 2005). An association between personality (as measured across three novelty tests) and feeding behaviour has also recently been demonstrated in dairy calves: More explorative and active individuals consumed solid food at an earlier stage and showed fewer visits to the milk feeder after weaning, suggesting a smoother transition from milk to solid food (Neave et al.,

2018). Other examples for the integration of personality measures into animal welfare science come from studies on judgement biases or on abnormal repetitive behaviour. In a judgment bias task, an animal’s decision in an ambiguous situation can be interpreted as either optimistic (in expectancy of something positive to happen) or pessimistic (in expectancy of something negative to happen) (Harding et al., 2004; Mendl et al., 2009), providing information about an animal’s affective state. Using such a judgement bias task, Lecorps et al. found that pessimistic responses were positively associated with fearfulness in dairy calves (Lecorps et al., 2018). Likewise, empirical studies at the interface between abnormal repetitive behaviours and personality traits have provided evidence for a positive relationship between measures characterising a proactive animal and the performance of stereotypies (Joshi and Pillay, 2016), and feather pecking in laying hens (Rodenburg et al., 2004) and parrots (van Zeeland et al., 2013). However, results were not always consistent or only held at the group but not at the individual level (Joshi and Pillay, 2016), highlighting the complexity of individual trajectories in the development of stereotypic and other abnormal repetitive behaviour.

Nevertheless, these examples show that animals can and do develop and potentially suffer from personality-dependent welfare problems. Thereby, some personality traits, such as aggressiveness, fearfulness, or risk-taking, seem to affect an individual’s welfare more strongly than other traits do at first glance. However, one may also speculate that personality differences in, for example, sociability or “caring behaviour” may also be strongly related to welfare as they influence the way animals respond to housing or weaning conditions. Future research would therefore benefit from a more in-depth exploration of traits that potentially affect welfare on various different levels. Furthermore, with respect to strategies to improve the welfare of animals in captivity, the close interaction between personality and welfare gives rise to the following two questions: Is it possible to design the animals’ environment in a way that allows good welfare for a variety of different personality types? Or can and should we select for animals with certain personality types that can be housed in captivity without developing welfare problems?

4.1. Creating one environment to fit all?

One can speculate, for example, that more explorative individuals may benefit from an environment including many novel items to discover, whereas less explorative animals may prefer to live in an environment full of places to hide. Likewise, reactive individuals may achieve good welfare in a rapidly changing environment, whereas environmental changes may have a negative impact on the welfare of proactive animals that tend to form set of routines and adapt to environmental changes more slowly (as suggested by Carere and Locurto, 2011). Indeed, some first studies in pigs indicate that the influence of rearing conditions on behaviour depends to some extent on coping characteristics of the individual animals (e.g., Bolhuis et al., 2004, 2006; Melotti et al., 2011). Furthermore, it has been shown that proactive individuals respond more optimistically in a judgement bias task, independent of their housing conditions, while the responses of reactive individuals depended on the animals’ housing conditions, with individuals provided with enrichment responding more optimistically than those housed without enrichment (Asher et al., 2016). What is beneficial for one individual is thus not necessarily beneficial for all individuals of a group, raising the question of how to create suitable and flexible housing environments with respect to both the enrichment and the grouping of individuals.

Animal welfare scientists currently explore the idea of challenges being a fundamental aspect of a life worth living (Meehan and Mench, 2007; Spinka and Wemelsfelder, 2018). Challenges in an otherwise barren and restrictive housing environment are supposed to promote competences and positive experiences as long as they are manageable and controllable. In line with this idea, studies in squirrel monkeys

(Parker et al., 2006) and humans (Seery et al., 2013) found that some challenge during development could indeed be advantageous rather than detrimental to an individual. This view is also supported by a recent study in laboratory mice showing that animals having experienced early beneficial and later escapable adverse conditions were characterised by a particularly low anxious phenotype (Bodden et al., 2015). Thus, a life without any challenge does not seem to imply a good life *per se*, but instead is likely to be experienced as monotonous, dull and boring (Sachser, 2001).

In line with this assumption, the integration of the “coping with challenge concept” in cognitive enrichment programmes has been shown to enhance the welfare of animals in captivity (e.g., Meehan and Mench, 2007; Spinka and Wemelsfelder, 2018). Studies on pigs, for example, tested a complex automatic feeding system in which pigs are individually called out to go to a feeding station (Ernst et al., 2005). Indeed, prolonged exposure to this system was found to alter the behaviour in a direction indicative of improved welfare and had also beneficial immunological and wound healing effects (Ernst et al., 2006; Puppe et al., 2007). At the individual level, however, it has been recognised that individuals respond differently to such challenges (Koolhaas and Van Reenen, 2016). Chimpanzees with higher scores in the personality trait “openness”, for example, were found to show higher levels of overall interest in a cognitive research programme in the zoo, indicating a personality-dependent effect on the adoption of such programmes (Herrelko et al., 2012). In particular, the success of the programmes seems to critically depend on intrinsic tendencies of an individual to interact with the environment as well as on the way challenges are experienced. To improve each individual’s welfare, enrichment programmes should therefore be designed in a way individual animals can flexibly choose between different options or be successful in cognitive tasks according to their individual needs. If applied in such a flexible way, cognitive challenge programmes may represent a promising approach to consider personality differences and at the same time improve the welfare of animals even at the individual level.

4.2. Selecting for specific individuals?

Individual variation has formed the basis for domestication and, over the centuries, specific breeding goals for different species have been defined. Several dog and cat breeds have been selected for specific morphological features (e.g., Bannasch et al., 2010; Drake and Klingenberg, 2008), whereas farm animals have mostly been bred for production traits, such as growth rate, milk yield or meat quality (e.g., Sandoe et al., 1999). Likewise, laboratory rodents have been bred to develop specific disease-related patterns, such as mammary tumours (e.g., C3H mice, Janvier Labs, 2018a) or spontaneous exocrine pancreatic insufficiency (e.g., CBA/J, Janvier Labs, 2018b). However, such approaches go hand in hand with the idea of selecting also for certain behavioural traits or personality types (e.g., D’Eath et al., 2010; Jones and Hocking, 1999; King et al., 2012; Rodenburg et al., 2010; Touma et al., 2008). The selection of silver foxes for tameability is probably the most famous example of successful breeding for behaviour (e.g., Trut, 1999; Trut et al., 2009). Even though only selected for tame behaviour, the selection process was accompanied by unexpected behavioural changes, such as maintained playfulness in adulthood (Elia, 2013), as well as morphological alterations, including brown mottling of the coat, floppy ears or curly tails (Trut, 1999). Further evidence for successful breeding for behaviour comes from studies on companion, farm, and laboratory animals. Sheep, for example, have been bred for improved maternal behaviour (Lambe et al., 2016), whereas beef cattle have been successfully selected for easiness in handling and reduced levels of aggressive behaviour (e.g., Le Neindre et al., 1995). Similarly, several studies have investigated the heritability of aggression-related traits across dog breeds (e.g., Liinamo et al., 2007; Pérez-Guisado et al., 2006), and in animal experimentation, mice have for example been selected to show signs of either high or low stress reactivity (e.g.,

Touma et al., 2008). Moreover, it has also been shown that it is possible to specifically tackle welfare-related problems, including breeding against abnormal repetitive behaviour, such as stereotypies (e.g., in mink: Jeppesen et al., 2004; in bank voles: Schoenecker and Heller, 2000) or feather pecking (e.g., in laying hens: Jensen et al., 2005; Rodenburg et al., 2010; van Hierden et al., 2002). Whereas selecting on behaviour (e.g. pecking behaviour) is supposed to be very time consuming, selecting for traits that are indicative of the damaging behaviour (e.g. plumage condition) might be more promising, especially if both the genetic effect originating from the actor (i.e. the pecker) and from its social partner (i.e. the victim) are taken into account (Ellen et al., 2014).

Breeding for behavioural change is not only limited because it is labour intensive but it also does not allow for qualitative but only, to a certain extent, for quantitative changes. Moreover, selection against specific behaviours might lead to animals that are inactive and simply unreactive to their environments, so-called “zombie animals”, or animals that still experience negative feelings but that do not show behavioural signs of suffering anymore, so-called “stoic animals” (D’Eath et al., 2010). In addition, breeding for or against certain behaviours might lead to reduced behavioural variation in a group of animals. Even though a group with animals of similar personality types may be beneficial for animal welfare since all individuals require more or less the same, we do not yet know all the risks going along with such reduced variation. Breeding for animals with certain characteristics might thus potentially improve animal welfare at the individual level, but the unknown consequences need to be considered very seriously and critically before changes in breeding programmes are implemented (D’Eath et al., 2010).

5. Part II - towards a stronger focus on the individual in animal welfare science?

As shown by these upcoming discussions about personality-dependent welfare problems, the concept of animal personality has already found its way into animal welfare science, indicating an increased awareness for unique features of individual animals. Despite this, however, the concept has mainly been implemented in experimental approaches in a somehow categorised way, i.e. by first identifying consistent inter-individual differences in behaviour and then comparing groups of individuals with different personality types (e.g., shy versus bold individuals). Thus, in contrast to the original idea of shifting the focus from the population to the individual, the personality idea is integrated by just adding another variance-explaining factor to the list, such as, for example, the age or the sex of the animals. Moreover, as the consistency of behaviour is one key element of the currently applied personality definition in behavioural ecology, most empirical studies address only those aspects of inter-individual behavioural variation that are consistent across time and/or context. However, the behaviour of an organism is known to be one of the most plastic of its phenotypic traits. Whereas the notion of personality suggests limited behavioural flexibility, this does not mean that animals are non-responsive to environmental changes (Nilsson et al., 2014). Complex interactions between the genotype and the environmental conditions an individual experiences over its lifetime can therefore result in huge phenotypic differences among individuals (e.g., Sachser et al., 2013). Integrating the concept of animal personality as currently defined by behavioural ecology into animal welfare science and studying consistent inter-individual differences in the aforementioned way is therefore just one step. Systematically addressing and investigating inter-individual differences beyond the personality concept is another one.

Looking at human psychology, inter-individual differences have repeatedly been highlighted as an important source for gaining crucial insights into the development and maintenance of specific diseases. Two recent reviews, for example, strengthened the role of the individual for the study of fear (Lonsdorf et al., 2017; Lonsdorf and Merz,

2017). Here, it has been argued that sample means do not necessarily describe individual response profiles in fear conditioning paradigms in a clinically relevant way. Alternatively, it has been suggested to investigate inter-individual differences systematically to understand why only some individuals develop pathological anxiety following traumatic events, while others do not (Lonsdorf and Merz, 2017). Although human and animal research may involve different complexity levels, the same logic potentially applies to animal welfare science since any kinds of behavioural response profiles can vary largely among individuals of the same sample. For example, environmental enrichment has repeatedly been shown to prevent or reduce the development of stereotypic behaviours in laboratory rodents, a finding that has mainly been based on group comparisons (e.g., Gross et al., 2011; Hadley et al., 2006; Powell et al., 2000). Thus, on average, mice housed in enriched conditions were found to display lower stereotypy levels than mice housed in barren environments, indicating that - at the mean level - housing conditions play a crucial role for the development of such abnormal repetitive behaviours. Looking at inter-individual differences, however, one realises that mice of the enriched conditions still differed greatly both in the type of performed stereotypy and in the overall frequency (e.g., Gross et al., 2011). The vulnerability to develop stereotypic behaviours therefore seems to vary greatly also between individuals living in the same environment, raising the question why some animals seem to be more prone to develop such abnormalities than others, a question that can partly be explained by consistent inter-individual differences, i.e. personality differences, but not completely.

Thus, focusing on the average responding of animals and treating variance in data as “noise” rather than meaningful information, deprives us from gaining crucial insights into welfare-related problems beyond the average. Given that individuals (and not only personality types) differ in their proneness to develop welfare problems in general and in the type of problems they suffer from specifically (Koolhaas et al., 2010), what does this mean for the study of animal welfare? Do we need to integrate the individual into the assessment? And what are the consequences for treating welfare-related problems of all animals of a group?

5.1. Beyond the average? Focusing on the individual in welfare assessment

Interestingly, the increasing awareness for the individual is widely reflected by new developments in legal requirements. Although most official regulations or guidelines aim to determine the minimum standards in a “one-size-fits-all” approach to guarantee at least a certain degree of welfare for all animals, single sections go beyond this philosophy and include the individual in the assessment. In the Directive 2010/63/EU of the European Parliament and of the Council on the protection of animals used for scientific purposes, for example, it is explicitly stated that “non-human primates, dogs and cats should have a personal history file from birth covering their lifetimes in order to be able to receive the care, accommodation and treatment that meet their individual needs and characteristics” (section 33, Directive 2010/63/EU). Furthermore, it is stated in Annex VIII of the Directive that “the severity of a procedure shall be determined by the degree of pain, suffering, distress or lasting harm expected to be experienced by an individual animal during the course of the procedure”. Likewise, the Animal Welfare Act from the UK strengthens the role of the individual by explicitly referring to “an animal’s needs” for a “suitable environment”, a “suitable diet”, and “to be able to exhibit normal behaviour patterns” (section 9, Animal Welfare Act, 2006). Whereas from an ethical perspective the focus on the individual animal is easily comprehensible, it comes with major challenges with respect to a proper welfare assessment. One basic requirement for a welfare assessment at the individual level is the ability of the responsible person to reliably distinguish between several individuals of a group. While this argument may sound trivial with respect to, for example, groups of primates, dogs or cats, it is far more complex or almost impossible for laboratory

rodents in huge animal facilities and many farm animals, such as fattening pigs, laying hens and broiler chickens. With respect to the latter, such welfare assessments are not only fundamental for describing the animals’ welfare states, but also for providing the basis for farm assurance schemes, thus directly or indirectly affecting consumers’ decisions which animal products to buy or not to buy (Main et al., 2001). Currently, farm assurance works at the farm or herd, not yet at the individual level, and improvements are implemented through pre-defined thresholds or benchmarking (Winckler, 2018). Although some of the collected information yield already information about individuals, as it is the case with lameness prevalence in dairy cows, the majority of measures stems from group assessments. In view of the large variation between single individuals, however, individual welfare assessments should be a future aim of farm assurance, as it is the premise to ensure the welfare of each animal. Thus, despite certain limitations especially with regards to feasibility, this further corroborates the importance of a more individual-tailored assessment and treatment of welfare problems in various different disciplines.

5.2. No more “one-size-fits-all”? An individual-tailored treatment of welfare-related problems

Whereas a focus on the individual animal may on the one hand pave the ground for an individual-tailored welfare assessment as discussed before, it may on the other hand stimulate research approaches towards an individual-tailored treatment of these problems. Generally, the idea that individuals can and should be treated according to their individual needs is not new. Looking at current developments in human health care, a novel keyword has found its way into the public consciousness. Under the terms “personalised medicine”, “individualised medicine” or “precision medicine”, scientists aim to customise medical treatment according to the individual genetic characteristics of each patient. As strong inter-individual differences in drug responsivity have repeatedly been linked to treatment failure or acute drug toxicity, the basic idea here is to improve the efficacy and safety of drugs by individualising the therapy (Evans and Relling, 2004; Ma and Lu, 2011). The focus has thus been shifted from a “one-drug-fits-all” approach to a patient-tailored intervention with the overall aim of optimising medical care and outcomes for each single individual (Annadurai et al., 2016; Liao and Tsai, 2013). A very similar approach exists in the veterinary practice. A significant proportion of companion animals develop behavioural problems, such as destructiveness, separation anxiety or aggression in dogs and house soiling or furniture scratching in cats (e.g., Heidenberger, 1997; Wells and Hepper, 2000). In order to prevent and treat such problems, behavioural therapies are typically tailored towards the individual animal, providing an example of an individualised therapy for animals in an every-day context.

Although not directly linked to welfare issues, intuitive or anecdotal knowledge about inter-individual differences in behavioural tendencies have also been incorporated into strategies to manage and exhibit animals in zoos. For example, anecdotal evidence has long been accumulated among black rhinoceros managers that aggressive behaviour can be linked to potential breeding problems in these animals. In an early multi-zoo study on the behaviour and breeding success of black rhinoceros, zookeepers were therefore asked to systematically describe the “behavioural style” of the rhinoceros they work with. Using these descriptions, indeed a negative correlation between certain dominant behaviours and reproductive success was found in male, but not female individuals. In line with the aforementioned intuitive knowledge, the authors came to the conclusion that a certain amount of aggressiveness and assertiveness may contribute positively to the females’ chances of breeding and that a submissive, adaptable and interactive style may be advantageous for males (Carlstead et al., 1999). Similarly, a recent study on courtship behaviour in the critically endangered European mink aimed at identifying individual behavioural indicators for detecting successful future breeders. Here, the male “clucking” sound was

found to be one of the best predictors for the later reproductive success: The more “clucking” sounds, the better the later reproductive success of this individual (Kneidinger et al., 2018). Likewise, such inter-individual differences have also been found to affect the way how individuals react to large numbers of zoo visitors (Stoinski et al., 2012) or the introduction of on-exhibit cognitive research training and testing (Herrelko et al., 2012), highlighting how important it is to incorporate knowledge about individual behavioural tendencies more formally in the successful management of these animals in zoos (Powell and Gartner, 2011; Tetley and O’Hara, 2012; Watters and Powell, 2012). As a non-scientific side effect, the realisation that animals express huge inter-individual behavioural differences may also help create greater empathy for animals in human hands, further enhancing public awareness and interest for welfare questions and conservation efforts (Smith and Blumstein, 2013).

6. Conclusion

Individuals do vary. Although this statement may seem trivial at first glance, it gave rise to the concept of animal personality, which – from our perspective – does have important implications also for animal welfare research. The systematic focus on (consistent) inter-individual differences in animal welfare research may provide additional valuable information beyond the investigation of pure group mean responses. In particular, account may be taken on the following aspects: (1) First, welfare is an individual outcome and as such, it is likely to be influenced by manifold interactions between an animal’s personality and the environmental conditions it experiences. Personality-dependent welfare problems can occur, raising further questions with respect to both the enrichment of the environment or the grouping of individuals that allows good welfare for a variety of different personality types, and the choice of individuals that can be housed in captivity without developing welfare problems. (2) Second, individual response profiles can reflect welfare-related problems “beyond the average”. This may stimulate research on an individual-tailored welfare assessment and contribute to an individual-tailored treatment of welfare-related problems, as it is known from modern human healthcare. Targeted research on this topic may thus indirectly and directly deepen our knowledge in animal welfare science and broaden the methodological repertoire used for the objective assessment of welfare. We therefore hope that this review stimulates more theoretical and empirical work and expands current research approaches to find ways of improving the welfare of animals in human hands even at the individual level.

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