

# Can We Assess Marine Mammal Welfare in Captivity and in the Wild? Considering the Example of Bottlenose Dolphins

Isabella L. K. Clegg<sup>1,2</sup> and Fabienne Delfour<sup>1,2</sup>

<sup>1</sup>Laboratoire d'Éthologie Expérimentale et Comparée EA.4443, Université Paris 13, Villetaneuse, France

E-mail: izziclegg@hotmail.co.uk

<sup>2</sup>Parc Astérix Delphinarium, Plailly, France

## Abstract

The welfare of a range of terrestrial animals can now be objectively estimated thanks to the well-established, but still expanding, field of welfare science. Despite continuing difficulties regarding definitions, it is generally agreed that welfare is assessed most accurately using multiple “animal-based measures”—that is, those evaluating aspects of the animal itself such as its behaviour. In addition, scientists combining behavioural, physiological, and cognitive animal-based indicators of welfare have found this approach is superior to using one-dimensional measures. But can the same approaches be used for marine mammals, and would assessments of their welfare have the same relevance in captivity as in wild environments? There is no reason why not, and we review the past decades of marine mammal research relevant to welfare, as well as the more recent advances in the field where this topic is starting to be addressed directly. We then use the example of bottlenose dolphins (*Tursiops truncatus*) to examine what the measures within an all-encompassing (i.e., “comprehensive”) welfare assessment might look like. Looking to the future, we suggest directions for developing assessments for captive animals and explore how protocols might differ in wild settings. In conclusion, we find that the first steps are being made towards objectively assessing marine mammal welfare in captivity—through application of terrestrial animal approaches as well as through novel paradigms. Regarding bottlenose dolphins, several welfare measures have been proposed and should now be further validated and applied. It is hoped that this review will encourage continued research in marine mammal welfare assessment given the demonstrated initial achievements of bottlenose dolphin welfare studies and the potential for application to many different captive and wild contexts.

**Key Words:** animal-based measures, animal welfare, bottlenose dolphins, *Tursiops truncatus*, marine mammals, welfare assessment

## What Is Animal Welfare Science?

### *Defining Animal Welfare*

The concept of animal welfare appeared rapidly on the public agenda in the 1960s after reports started to emerge detailing the conditions within intensive farming systems (Veissier et al., 2008). The study of animal welfare has since been established and expanded to laboratory, companion, and now zoo-housed animals (Webster, 2005; Whitham & Wielebnowski, 2013). Numerous definitions of animal welfare were proposed during this time that generally fell into either “health-based,” “natural-living,” or “feelings-based” definitions, depending on which of these three factors researchers thought to be most influential to the overall state of welfare (Fraser et al., 1997). Although a single definition has still not been agreed upon, there seems to be a general consensus that welfare is predominantly concerned with how the animal is *feeling* (Broom & Fraser, 2015; Dawkins, 2015). Health can of course greatly influence welfare through altering how an animal feels, and a “natural” way of life is relevant in certain situations and, thus, is still included in some welfare paradigms. However, “feelings-based” definitions of welfare are most often adopted in studies independent of the species concerned (Bracke et al., 1999; Spruijt et al., 2001; Boissy et al., 2007; Yeates & Main, 2008; Mason & Veasey, 2010; Watters, 2014).

In this review, we also advocate that an animal’s welfare concerns how it is feeling, and we follow the specific definition proposed by Spruijt et al. (2001), which states that welfare is “a balance between positive (reward, satisfaction) and negative (stress) experiences or affective states. The balance may range from positive (good welfare) to negative (poor welfare)” (p. 159). When

welfare state is considered as a product of an animal's feelings, the study of emotion and affective states becomes key in developing welfare measures and assessments (Désiré et al., 2002; Boissy et al., 2007; Yeates & Main, 2008). Affective states are defined as *free-floating mood states*, resulting from shorter-term emotions and feelings stimulated by the individual's environment, and research on these phenomena in humans and other species has guided the principles used when assessing animal welfare (Russell, 2003; Paul et al., 2005; Mendl et al., 2010).

### *Principles of Assessing Welfare*

Welfare science has many applications for improving the lives of animals kept by humans. To promote good welfare and avoid poor welfare for an animal, we must be able to measure welfare objectively. It is worth noting here that a fundamental aspect of assessing welfare is its inherent subjectivity. In fact, we will never be able to completely and accurately measure this subjective and transitional state. However, this should not deter researchers since the use of many multidimensional indicators over a sufficient time frame can certainly lead us to informed estimations of an animal's level of welfare (Dawkins, 2006; Blokhuis, 2008). Thus, the second key principle of measuring welfare is that it is a holistic, all-encompassing phenomenon that should thus be assessed using multidimensional measures (Whay et al., 2003; Boissy et al., 2007; Yeates & Main, 2008). The main categories of these different measures are behaviour, physiology, and cognition since they are also the three components of emotional responses (Désiré et al., 2002; Paul et al., 2005). Webster (2005) explained the function of multiple measures using the *Triangulation* principle, wherein the three components of welfare measures are points on a triangle, and the true centre is the animal's actual welfare: the predicted welfare state starts on one of the points when we have information from a one-dimensional measure, and adding second and third bearings (measures from other components or "dimensions") brings the predicted welfare ever closer to the centre. So, when developing a welfare assessment (a group of welfare measures), researchers include measures from different dimensions to capture as much information about the animal's internal state as possible and, thus, make a more accurate evaluation of welfare (Whay et al., 2003; Pritchard et al., 2005; Clegg et al., 2015).

In the past, welfare research and assessments have been heavily focussed on identifying signs of poor welfare in animals, where good welfare was thought to result from an absence of suffering (Dawkins, 1980; Broom & Johnson, 1993). As data and practical knowledge have increased regarding

this topic, and perhaps also due to the relatively recent acceptance that animals are indeed likely to experience a range of emotions and affective states, it is now agreed upon that positive emotions and welfare should be measured and promoted as part of good practice protocols (Boissy et al., 2007; Yeates & Main, 2008; Mellor & Beausoleil, 2015). Thus, more recent welfare definitions, such as that of Spruijt et al. (2001) followed in this review, discuss a continuum of poor to good welfare for which the balance of positive and negative experiences dictates the welfare state at a given point in time (Boissy et al., 2007; Yeates & Main, 2008; Watters, 2014).

Another aspect of welfare assessments is that two different types of welfare measures are generally used: (1) animal-based measures (data are taken directly on the animal's behaviour and health, for instance) and (2) resource-based measures (data taken from resources provided to animal, e.g., enclosure space). Resource-based measures were used more frequently in earlier assessments and research because they are more practical and easier to standardise (Whay et al., 2003; Veissier et al., 2008). Although resource-based welfare measures still constitute welfare laws and regulations in most cases (e.g., for zoo animals: Animal Welfare Act, 1966; EC Council Directive, 1999), data yielded from animal-based measures are now considered to be more accurate indicators of an animal's welfare (Dawkins, 2006; Whitham & Wielebnowski, 2009; Roe et al., 2011).

General welfare paradigms, such as the *Five Freedoms* (Farm Animal Welfare Council [FAWC], 1992) or the *Five Domains* (Mellor & Reid, 1994), which detail the different aspects of any animal's life in general terms, are often used to select and organise the measures included within species-specific welfare assessments (Welfare Quality®, 2009a; Mononen et al., 2012; Clegg et al., 2015). After the initial proposal for an assessment, the validity of the selected measures should be confirmed—that is, are they measuring what they intend to measure (Rushen, 2003). Validation is usually conducted in separate studies from which a few potential measures from different disciplines (e.g., behavioural and physiological) may be applied concurrently to animals in contexts of highly likely poor and/or good welfare (Désiré et al., 2002; Castellote & Fossa, 2006), or through using large-scale epidemiological data (Rushen, 2003). In a significant advance for animal welfare science, a novel technique from human experimental psychology through which the *cognitive bias* of an animal is tested has also been shown to be able to validate welfare measures (Harding et al., 2004; Mendl et al., 2010). Cognitive biases, which are present in humans and animals, describe the effect an individual's emotional state has on

cognitive processing (e.g., making a judgment). For example, it has been shown in a wide range of species that when placed in poorer welfare situations, more pessimistic judgments are made and vice versa (latest reviews by Baciadonna & McElligott, 2015; Roelofs et al., 2016). Therefore, correlating animals' cognitive biases to potential indicators of welfare is starting to be used as a method of validation (e.g., Wichman et al., 2012; Clegg et al., 2017a).

#### *Examples of Welfare Assessments*

The key principles above are integrated in several established welfare assessment protocols, mostly within the farming sector. The 2004 Welfare Quality® project developed extensive welfare assessments of 30 to 50 measures for farmed pigs (*Sus scrofa domesticus*), cattle (*Bos taurus*), and laying hens (*Gallus gallus domesticus*) (Welfare Quality®, 2009a, 2009b, 2009c), which are slowly being incorporated into codes of best practice and European strategies (Blokhuys et al., 2010). While the individual measures were species-specific, the overarching principles and criteria of the Welfare Quality® Assessments can be adapted to other animals (Botreau et al., 2012), and this first occurred for farmed foxes (*Vulpes* spp.) and mink (*Neovison vison*) (Mononen et al., 2012), and more recently shelter dogs (*Canis lupus familiaris*) (Barnard & Ferri, 2015) and bottlenose dolphins (Clegg et al., 2015). The Welfare Quality® framework is seen by the field as a comprehensive, standardised, and practical way to measure animal welfare, but one which needs more development on aspects such as assessing emotional states (Botreau et al., 2007; Mellor, 2016).

The Welfare Quality® project has been the most ubiquitous and well-validated effort towards establishing welfare assessments (Blokhuys et al., 2010; Veissier et al., 2013); nevertheless, there are other approaches which have also garnered support. One of these is the *Five Domains Model*, which is fundamentally based on the *Five Freedoms* but differs in that it facilitates measurement of the *degree* of the impaired freedom (poor welfare) (Mellor, 2016). Developed in New Zealand, this model has been incorporated in the country's regulations for research, teaching, and testing manipulations, and it is being worked on further to allow measurement of positive affective states as well (Mellor & Beausoleil, 2015). The Welfare Quality® Assessments and the *Five Domains Model* have been used almost exclusively in the farming and laboratory animal industries; and apart from the C-Well® Assessment for bottlenose dolphins (Clegg et al., 2015), there are very few examples of animal-based, comprehensive assessments for zoo-housed species. Instead, resource-based questionnaires with unvalidated

measures are often used (e.g., Draper & Harris, 2012). However, there is a noteworthy amount of zoo research that has been conducted on single measures of welfare that could be developed to be included in overall assessments, including cortisol measurement (Menargues et al., 2008), stereotypic behaviour (Shepherdson et al., 2013), and qualitative keeper assessments of behaviour (Whitham & Wielebnowski, 2009). In general, studies in this setting are making significant progress towards rendering potential welfare indicators "measurable," such as the recent work on the play behaviour of African elephants (*Loxodonta africana*) (Vicino & Marcacci, 2015), and others are starting to validate chosen measures by correlating them with other welfare data (e.g., using behavioural and physiological indicators; Pifarré et al., 2012; Baird et al., 2016). Encouraging discussions have also started on establishing universal zoo welfare frameworks that include more animal-based measures (Kagan et al., 2015).

Regarding animals in the wild, it is only just being acknowledged that assessing their welfare is even possible or worthwhile, despite some protagonists pointing out the significant benefits that measuring welfare could have for conservation projects, public outreach, and the animals themselves (Kirkwood et al., 1994; Paquet & Darimont, 2010; Papastavrou et al., 2017). There are, however, a few examples of studies teaming welfare science principles to wild marine animals. For example, the issue of marine debris was examined in terms of impacts on individual animal welfare (Butterworth et al., 2012). A recent review was conducted outlining specific measures that might be applied to wild dolphin welfare assessments (Clegg et al., 2017b). Finally, with the aim of establishing effective conservation protocols for cetaceans, the International Whaling Commission (IWC) proposed a *Five Domains Model* adapted to wild cetaceans (Butterworth, 2017b). Therefore, although wild animal welfare measurement is only just emerging in the scientific domain, the applications for marine mammals and their conflicts due to anthropogenic causes seem to be high on the agenda (Papastavrou et al., 2017).

Given the progress in the field and the approaches to welfare assessments discussed above, we see no reason why such developing welfare measures should not be achieved for marine mammals. In the next section, we examine whether any welfare measures exist already and compile those studies that have been conducted on topics that are closely related to marine mammal welfare. Since welfare research on bottlenose dolphins is the most advanced (Clegg et al., 2017b), we use examples of measures for this species where appropriate.

## What Research Has Been Conducted on Marine Mammal Welfare?

### *Early Studies Linked to Marine Mammal Welfare*

Despite the recent public and media attention surrounding marine mammal welfare in captivity (Jiang et al., 2007; Ventre & Jett, 2015), very few studies have posed direct questions on how to measure these animals' quality of life (Ugaz et al., 2013; Clegg et al., 2017b). However, while not explicitly investigating animal welfare, there are many studies on wild and captive marine mammals that focus on measures relevant to welfare and could one day be included in overall assessments. Reviews compiling the literature relevant to potential welfare measures for cetaceans and pinnipeds can be found elsewhere (see, respectively, Clegg & Butterworth, 2017a, 2017b). Herein, we examine the progression of welfare-focussed research on marine mammals to understand where the next advances in the field might occur.

While the study of marine mammals has been well-established for decades, research effort is biased towards certain topics and certain species. For example, cetaceans, bottlenose dolphins, and killer whales (*Orcinus orca*) are the most investigated and are the marine mammals for whom the topics of health, physiology, and distribution are predominantly focussed (Hill & Lackups, 2010; Hill et al., 2016). Therefore, welfare-related findings in past studies can be found but are not representative of all marine mammal species or all aspects of welfare measurement. Many early studies in the wild and captivity that looked at stress hormone concentrations in different species (e.g., in harbour seals [*Phoca vitulina*]: Riviere et al., 1977; and bottlenose dolphins: Thomson & Geraci, 1986) have helped to build baselines for indicators such as cortisol levels, which have been used as a welfare measure for farm and domestic animals (e.g., Carlstead et al., 1993; Gimsa et al., 2012). Health and other physiological parameters were often investigated in early wild and captive studies; and as a result, there are many reviews on disease symptoms and prevalence in marine mammals (see Dunn et al., 2001; Miller et al., 2001; Van Bressen et al., 2008). Although social and other behaviours appeared less frequently in the literature, long-term studies were starting to establish themselves and used their identification abilities and life-history knowledge of populations to publish on welfare-relevant topics such as affiliative and aggressive behaviour (Herzing, 1996; Herzing & Johnson, 1997) and reproductive behaviour (reviewed in Wells, 2009).

In the 1990s, the first marine mammal studies to use the term *welfare* emerged, and although the animals' feelings were still not discussed, there

was a much stronger focus on behaviours that later have been shown to be linked to emotional states (Kastelein & Wiepkema, 1988; Gyax, 1993; Galhardo et al., 1996). A few years later, a study on bottlenose dolphins explicitly attempted to identify indicators of poor welfare, finding that social isolation, inappetence, changed relationships with humans, and increased rake marks all resulted from severe social stress (Waples & Gales, 2002). An investigation into the acoustic behaviour of two belugas (*Delphinapterus leucas*) found that vocalisation rate decreased temporarily after transportation to a new facility, leading it to be suggested as a welfare indicator (Castellote & Fossa, 2006). In the next decade or so, perhaps due to the rise of environmental enrichment programs in zoos and aquaria (Hoy et al., 2010), a large proportion of marine mammal welfare research focussed on enrichment provision (e.g., Grindrod & Cleaver, 2001; Kuczaj et al., 2002).

### *Marine Mammal Enrichment Studies and Their Relevance to Welfare*

When *enrichment* is defined precisely—as the addition of stimuli or the provision of choices designed to stimulate any one or more of the senses (Azevedo et al., 2007)—it does not necessarily impact the welfare state of the animal. A more general definition often used is that enrichment is any husbandry activity that *aims* to improve animals' well-being, and this is often misconstrued, resulting in enrichment being considered as something that always improves welfare (Hoy et al., 2010). In addition to being inaccurate, this assumption has resulted in enrichment programs and related research often not attempting to measure the welfare impacts (Newberry, 1995; Hoy et al., 2010). Marine mammals live in an environment very different to our own where they enact subjective worlds (Delfour, 2010b); and as humans, we continue to make anthropocentric assumptions about which enrichment items *should* increase welfare the most. Unfortunately, we are often wrong—for example, bottlenose dolphins played more with simple versus complex enrichment objects (Delfour et al., 2017). The last problem is that since validated welfare indicators are sparse for most species (Rushen, 2003), even if enrichment studies want to measure the welfare impacts, the tools to do so are often lacking (Clegg et al., 2015).

So, what have marine mammal enrichment studies shown so far, and can they be relevant to welfare measurement? In the 1990s and 2000s, several studies published data on providing enrichment to captive marine mammals. “Toy” objects (Kuczaj et al., 2002), acoustic stimulation (Berglund, 2005), pool design changes (Krajnaik,

1996), and cognitive challenges (Reiss, 2006) have been presented to dolphin species, and all of the above to pinniped species (e.g., Kastelein & Wiepkema, 1989; Wassel et al., 1996; Grindrod & Cleaver, 2001). In most of these studies, the time spent with the items is measured and, according to a subjective assessment, the authors conclude that the enrichment is “successful”; however, can we say that animal welfare has been improved? Later in the 2000s, we started to realise far more detailed assessments would have to take place to discover whether enrichment was actually leading to good welfare, and a number of papers provided some direction for how to achieve this in marine mammals (Delfour & Beyer, 2012; Clark, 2013; Clegg et al., 2015). Subsequently, recent studies are more often conducting meticulous analyses of the animal-based impacts of enrichment; and by using this work, we can see that enrichment indeed has the potential to promote positive welfare states in marine mammals. For example, Australian sea lions (*Neophoca cinerea*) showed less stereotypic swimming after toy objects were introduced (Smith & Litchfield, 2010), and Australian fur seals (*Arctocephalus pusillus doriferus*) showed higher behavioural diversity after foraging-based enrichment was applied (Hocking et al., 2015). The diversity of belugas’ play behaviours increased when enrichment items were present (Hill & Ramirez, 2014), and bottlenose dolphins interacting with a cognitive enrichment device then became more interested in the underwater aspect of their home environment (Clark et al., 2013). These studies measured potential animal-based measures of welfare during enrichment to suggest that it has positive effects. After further validation of such measures, these correlations could aid future welfare studies for which the proven “positive impact” of enrichment devices could be used to simulate positive affective states (Clegg & Butterworth, 2017a).

#### *Recent Advances: Comprehensive Assessment of Marine Mammal Welfare*

In the last few years, the advances made in terrestrial animal welfare science seem to have led to a notable increase in the amount and quality of investigations with marine mammals. In particular, we are seeing the first studies attempting to measure marine mammal welfare using multidimensional, animal-based measures of both positive and negative welfare leading to more comprehensive, holistic evaluations. A multi-facility study found bottlenose dolphins had higher levels of cortisol when kept in a closed versus open system, which itself was correlated to higher levels of floating and circular swimming (Ugaz et al., 2013). A welfare assessment protocol for dolphins was developed by Clegg et al. (2015), representing the first application of an operational farm animal assessment

within the zoo industry. The framework, termed the *C-Well*® Assessment, was adapted to bottlenose dolphins from the well-established Welfare Quality® Assessments (2009a, 2009b, 2009c). First, species-specific measures were proposed using the literature and tested for face validity using expert opinion. They were then tested for feasibility on 20 bottlenose dolphins from three facilities and were partially validated using contexts such as sick animals or social disturbances. The *C-Well*® Assessment is made up of 36 multidimensional measures, 58% of which are animal-based, and produces individual welfare scores which can be compared on many levels such as by age, sex, group, or facility. However, the assessment needs more work to fully validate the measures, which are also currently unweighted. Nevertheless, the project developed standardised methods and scoring thresholds for measuring dolphin welfare and represents a first step towards practical assessments in zoo settings.

Concurrently, separate studies from different research groups have been conducted on measures which are included in the *C-Well*® framework or closely related. For example, advances have taken place in our understanding of dolphin play and affiliative behaviours, which are commonly used indicators of positive welfare in other species (Boissy et al., 2007; Held & Špinka, 2011) in terms of influencing factors (Dudzinski & Ribic, 2017; Harvey et al., 2017; Serres & Delfour, 2017) and the links with emotion (Paulos et al., 2010; Kuczaj et al., 2013). Research reporting the first cognitive bias tests conducted with marine mammals show that optimistic decisions in bottlenose dolphins were correlated to higher levels of synchronous swimming in their free time, suggesting that following further investigation, this affiliative behaviour could be used as an objective welfare indicator within assessments (Clegg et al., 2017a). Holistic assessments of pinniped and other marine mammal species’ welfare are notably less common than for cetaceans. A unique report on sea lion species’ welfare in circuses started the discussion for pinnipeds; and although consensus was reached among experts regarding the important resource-based measures, there was much variation on the animal-based evaluations, and it was concluded that more research was urgently needed (Hopster & de Jong, 2014). In one of the first references to emotions and pinnipeds, a study recently found some indications that motor lateralisation was caused by changes in emotional state in captive California sea lions (*Zalophus californianus*), but again, more research is needed before conclusions are able to be made for welfare or its measurement (Le Ray et al., 2017).

There has also been some movement in wild marine mammal research towards developing welfare assessments. Recently, it has been

promulgated in multiple reviews that such assessments would greatly aid conservation and ecological objectives (Paquet & Darimont, 2010; Papastavrou et al., 2017; Seuront & Cribb, 2017). Perhaps in response to these recommendations, the IWC has taken a large step forward and is in the early stages of developing a comprehensive assessment for wild cetaceans using the *Five Domains Model* to develop measures for as many aspects of the animals' lives as possible (Butterworth, 2017b). Given the advances in marine mammal welfare research described above, there have also been multiple reviews recently published on what types of specific measures might be included in cetacean (Clegg & Butterworth, 2017a; Clegg et al., 2017b) and pinniped (Clegg & Butterworth, 2017b) welfare assessments in both wild and captive settings.

Therefore, in answer to the question of whether marine mammal welfare is already being studied, we can see that (1) decades of research on unidimensional but relevant measures are slowly starting to be gathered together and integrated, (2) farm animal welfare techniques are being trialled and adapted successfully in captive settings, and (3) the first few examples of comprehensive assessments are emerging but by no means well-established. We will now further investigate what the exact measures within a welfare assessment might be and how they would be conducted. For this, we will use the bottlenose dolphin as a specific example since the species has the most research available in this area.

### What Are Some Potential Welfare Measures of Bottlenose Dolphin Welfare?

While the potential measures are reviewed separately in this section, the objective would always be that they are conducted as part of a comprehensive assessment as this is the most accurate way to measure welfare (Bracke et al., 1999; Webster, 2005; Botreau et al., 2007). The measures are organised into three main categories according to the Triangulation principle discussed earlier (Webster, 2005): (1) physiology, (2) behaviour, and (3) cognition. Although health parameters are not thought to be directly involved in emotional responses, we start by examining their utility in welfare frameworks for bottlenose dolphins.

#### *Health Parameters in Relation to Welfare*

Since welfare science was born out of veterinary medicine, welfare evaluations were traditionally linked closely with the health status of an animal (Dawkins, 2006). More recently, and especially for those adopting the "feelings-based" definitions of welfare as we have here, it is common

to only consider health problems of animals in terms of their impact on emotional and affective states (Fraser et al., 1997; Mason & Veasey, 2010; Clegg et al., 2017b). In other words, an asymptomatic tumour with no resulting pain would not be considered to cause poor welfare in an animal, but an infection that results in inappetence, pain, and sickness could indeed be used as an indirect measure of poor welfare. Nevertheless, the relationship between health and affective states is complex and not fully understood in humans or animals: negative affective states have a potential impact on morbidity, mortality and longevity (Walker et al., 2012). Therefore, we consider a few key health measures that might be linked to bottlenose dolphin welfare (for a larger review, see Clegg et al., 2017b).

The main impacts of an infection or disease on an animal's affective state are pain and/or "sickness behaviour," which describes a suite of effects including inappetence, lethargy, depression, and anti-social behaviours (Broom, 1991; Millman, 2007; Sneddon et al., 2014). Therefore, developing measures for these indicators of poor health would certainly be useful as part of welfare assessments and would be feasible for sickness behaviours. Pain is more difficult to measure in dolphins since they are known to mask their symptoms for adaptive reasons (Waples & Gales, 2002; Castellote & Fossa, 2006), and, thus, proxy measures of pain may have to be used such as the severity of injuries or a developmental stage of the disease (as proposed in Clegg et al., 2015). Body Condition Scoring (BCS) is used in many farm animal welfare assessments (Welfare Quality®, 2009a, 2009b, 2009c; Mononen et al., 2012) since it is a good overall reflection of health status. BCS has been used in wild cetacean health assessments (Hart et al., 2013; Joblon et al., 2014) and was also suggested as a bottlenose dolphin welfare measure (Clegg et al., 2015). In settings where individual welfare measures are not possible (i.e., for some wild populations), epidemiological measures such as morbidity and reproductive success can still give us some idea of health and possibly welfare (Dawkins, 1998; Barber, 2009). Since such measures are not always accurate welfare indicators (e.g., fecundity in farm animals), the most effective use of epidemiological data are in conjunction with other animal-based measures (Dawkins, 1980). For example, a recent study on minke whales (*Balaenoptera acutorostrata*) found correlations between disturbance behaviour from whale-watching boats, body condition, and foetal growth (Christiansen & Lusseau, 2015), thus rendering foetal growth a meaningful welfare measure for when the other sources of data are not available. More studies are needed, and more data needs to be published, on baselines for epidemiological

parameters in captivity and in the wild to supplement those available (for *T. truncatus*: Small & Demaster, 1995; Innes et al., 2005; Reif et al., 2008; Schwacke et al., 2014) before such measures would be deemed valid enough to use as welfare indicators.

### *Physiological Welfare Measures*

In terms of welfare assessment, physiological measures (e.g., cortisol levels and breathing rate) are differentiated from health parameters in that they function to measure the physiological component of emotional responses (Désiré et al., 2002; Boissy et al., 2007). Physiological measures are advantageous as they can indicate emotional responses which are not obviously seen in the animal's behaviour, and they enable us to differentiate between behaviours performed to satisfy a "need" (e.g., finding food to reduce hunger and increase blood glucose levels) and those performed with no link to short-term physiological needs (e.g., grooming) (Boissy et al., 2007). While physiological indicators are often used in individual studies on farm animal emotions and welfare (Reefmann et al., 2009; Leliveld et al., 2016), not many are included in comprehensive welfare assessments due to problems with feasibility and standardisation of equipment (Velarde & Dalmau, 2012; Veissier et al., 2013). However, this could be a distinguishing point between farm and zoo animal welfare assessments since the former are often conducted on large groups and with limited means of identifying individuals; while for the latter, it is more feasible and often desirable that welfare is measured per individual (Barber, 2009; Clegg et al., 2015). In addition, the "trainability" of captive marine mammals (Brando, 2010) would allow many physiological measures to be conducted non-invasively (when farm animals would need restraint or sedation), and, thus, physiological measures might have a prominent role in bottlenose dolphin welfare assessment. Unfortunately, there are very few physiological measures of emotion which have been sufficiently studied in dolphins to merit their inclusion in a welfare assessment; and, thus, for the moment, we can only outline a few that may be useful pending further research.

Measuring cortisol levels (or those of its derivatives) is one of the most common physiological indicators of stress used with captive terrestrial animals (e.g., Bachmann et al., 2003; Hekman et al., 2012; Palme, 2012) and those in the wild (e.g., Tarlow & Blumstein, 2007; Bechshoft et al., 2012). For bottlenose dolphins, cortisol concentrations can be measured from serum or plasma after blood sampling (Thomson & Geraci, 1986; Ortiz & Worthy, 2000), and more recently from urine, faeces, and saliva (Pedernera-Romano et al., 2006; Fair

et al., 2014; Biancani et al., 2017). Cortisol measurement was proposed as a measure in the C-Well® Assessment of Clegg et al. (2015), and a few studies are available showing potential correlations to welfare (e.g., Ugaz et al., 2013). The most significant of these was able to demonstrate that an increase in salivary cortisol could be detected on days in which construction work was being conducted near to the dolphin pool (Monreal-Pawłowsky et al., 2017). In addition, there is still the ubiquitous problem that cortisol concentrations vary diurnally, and we have not established reference baselines (Atkinson et al., 2015). Nevertheless, studies are continuing to work towards understanding the different sources of variation, and it would be prudent to "watch this space" for progress on using cortisol levels as a welfare measure for this species.

Other potential physiological measures linked to welfare could be those linked towards respiration rate and depth. An increased breathing rate has been shown in response to boat traffic in wild dolphin populations (e.g., Janik & Thompson, 1996; Nowacek & Wells, 2001) and is thought to be a sign of stress in captive dolphins (St. Aubin & Dierauf, 2001; Jensen et al., 2013). However, no link was found between breathing rate and cortisol concentration in wild harbour porpoises (*Phocoena phocoena*); and since in bottlenose dolphins, breathing rate also increases with energetic output (Williams et al., 1999), this parameter might only be useful in terms of welfare as a measure of arousal. Other aspects of respiration, such as inhalation duration or frequency of coughing, could be useful health-related measures as they can indicate respiratory disease (Dunn et al., 2001; Clegg et al., 2015). To fully understand the impact of respiratory disease on the animal's affective state, however, further work is necessary. Physiological measures such as heart rate and heart rate variability have been used to assess farm animal emotions (Rietmann et al., 2004; Coulon et al., 2015) but have not yet been applied in dolphin welfare investigations.

### *Behavioural Welfare Measures*

Studying certain behaviours from an animal's repertoire is increasingly believed to be the most informative approach to measuring welfare (Gonyou, 1994; Maple, 2007), and this is likely also true for marine mammals (Joseph & Antrim, 2010; Clegg et al., 2017b). In general, there are still many unknowns regarding marine mammal behaviour and its ontogeny (Hill & Lackups, 2010), so further ethological studies on a range of species in the wild and captivity would certainly aid the development of welfare measures. Regarding bottlenose dolphins in particular, those welfare indicators labelled as having potential are almost all behavioural measures, and we discuss the most significant of these below.

*Social Behaviours*—Bottlenose dolphins, like many other delphinid species, live within complex social networks (Shane et al., 1986; Wells, 1991) and are dependent on close social bonds for survival (Pack & Herman, 2006; Stanton & Mann, 2012). Whether in the wild or captivity, this means they are more likely to suffer from social stress than animals that rely less on social bonds and group living situations (Waples & Gales, 2002). At the same time, they also may have greater opportunities for achieving positive welfare states as a result of strong bonds with others and stress buffering (Clegg et al., 2017b).

The significant role of social stress in causing poor welfare states has been documented in a variety of species and contexts (e.g., Shively et al., 1997; Sapolsky, 2005; Papciak et al., 2013). One study found social stress to be the likely cause of mortality and morbidity in three bottlenose dolphins, caused by social instability and the consequent aggressive interactions (Waples & Gales, 2002). As suggested by the authors, indicators such as social isolation, inappetence, high aggression levels, and extensive rake mark coverage could be used as measures of social stress, and likely for poor welfare as well. Rake marks have been proposed in a number of other cases as a proxy measure for aggression since many aggressive encounters go unseen when studying wild and captive dolphins (Scott et al., 2005; Marley et al., 2013), and the percentage of new rake marks could be an objective way to measure this aspect of welfare (Clegg et al., 2015). Using actual levels of aggressive behaviour could also be a possible measure since this is used in the Welfare Quality® frameworks (2009a, 2009b, 2009c), but more investigation would be needed into whether both acting and receiving aggression are linked to negative affective states or whether the relationship between dominance, subservience, and stress is more complicated as in some primate species (e.g., Abbott et al., 2003; Sapolsky, 2005).

In terms of how social behaviour can lead to positive welfare in animals, it is thought activities such as close bonds, cooperative behaviour, and prosocial tactile interactions (e.g., grooming and play) lead to positive affective states; however, it is relatively difficult to prove this (Boissy et al., 2007; Yeates & Main, 2008; Mellor & Beausoleil, 2015). Regarding dolphin species, our knowledge of affiliative social behaviour is relatively well-established thanks to studies in the wild (long-term studies particularly, e.g., Herzing, 2000; Connor et al., 2006b), captivity (Tamaki et al., 2006; Harvey et al., 2017), and those that have compared both (Dudzinski, 2010; Dudzinski et al., 2012). There are a few behaviours that have been proposed to have links to positive emotions but have not yet been validated in this way—for example, pectoral

rubbing and contact is thought to reflect social bonds (Kuczaj et al., 2013; Dudzinski & Ribic, 2017) and has been shown to decrease the likelihood of aggressive behaviour (Tamaki et al., 2006), and so could be investigated as a measure of positive welfare.

Social play is a prosocial behaviour generally taken to reflect positive welfare since it is thought to occur only when an animal's primary needs have been satisfied (Held & Špinka, 2011; Bateson, 2014), although some caution has been advised regarding its measurement and the fact that play can evolve into bouts of fighting (Boissy et al., 2007). Studies have confirmed that this is also the case with dolphin play (see review by Kuczaj & Eskelinen, 2014), and recent progress was made towards using it as a welfare measure when researchers found captive bottlenose dolphins conducted less social play when noisy construction work was occurring next to the pool or agonistic interactions had taken place (Serres & Delfour, 2017). The most meaningful way to measure dolphin play remains unclear (Serres & Delfour, 2017), and attempts could be made to develop and validate an index such as that used for African elephants by Vicino et al. (2015).

Synchronous swimming, when two or more dolphins swim in parallel, mirroring each others' movements, is perhaps the affiliative behaviour with the most convincing research supporting it as a welfare measure thus far. This behaviour reflects social bonding in wild and captive dolphins (Connor et al., 2006b; Holobinko & Waring, 2010; Sakai et al., 2010), and was found to be correlated to optimistic judgements made by captive dolphins in a study testing cognitive bias (Clegg et al., 2017a). Optimistic judgement biases are known to be linked to positive affective states, and the experimental paradigm is one of the only well-validated tests of welfare (Mendl et al., 2009, 2010). Further investigations are still needed into this measure, however, since synchronous swimming can also be shown in stressful contexts during which it acts as a form of social support (Connor et al., 2006a). Differentiating this behaviour by speed and distance to partner could lead to certain types of synchronous swimming being used as welfare indicators (Clegg, 2017).

Lastly, interspecific social behaviour towards humans can reveal much about an animal's welfare (Whitham & Wielebnowski, 2009; Hosey & Melfi, 2014) as well as representing an opportunity to induce positive affective states itself (Hemsworth, 2007; Whitham & Wielebnowski, 2013; Coulon et al., 2015). Despite captive marine mammals often having close working relationships with their caretakers and sometimes unfamiliar guests, which can involve much time spent in close contact with each other, the human–animal relationship (HAR) is studied very little in this setting



(Clegg & Butterworth, 2017a). Past results have been mixed regarding dolphin behaviour towards unfamiliar guests swimming with them (Frohoff & Packard, 1995; Kyngdon et al., 2003; Trone et al., 2005). Concerning their familiar trainers, a study showed that bottlenose dolphins voluntarily sought tactile contact out of feeding sessions (Perelberg & Schuster, 2009), while another recent investigation confirmed that they positively anticipated non-food tactile interactions with trainers and more than the provision of enrichment (Clegg et al., 2018). This partially validates the comparable HAR measure included in the C-Well<sup>®</sup> Assessment (Clegg et al., 2015), based on a simple approach-avoidance test used for farm animals (De Passillé & Rushen, 2005). More work is needed on this aspect of captive dolphins' lives since training sessions and public presentations make up a large part of their daily routine (Clegg et al., 2017c), and results may be able to aid in developing similar welfare measures regarding human-animal interactions in the wild.

*Solitary Behaviours*—A dolphin's responses to its surrounding environment and its solitary activity might also reflect its welfare state. Following the above discussion on social play, it is likely that solitary play also reflects positive emotions (Held & Špinka, 2011). However, although not often studied as such, it could be that the two types of play have different functions (Greene et al., 2011) and, therefore, may be better considered as separate welfare measures in the future. Bottlenose dolphins are known to play on their own with objects and by producing bubbles (McCowan et al., 2000; Delfour et al., 2017), so further work on the contexts where the different play behaviours are seen would be valuable (Greene et al., 2011; Kuczaj & Eskelinen, 2014). In terms of links with welfare, stereotypic behaviour involves solitary activity (in most cases) which has been found in many species to reflect an understimulating environment (Mason & Rushen, 2006). Unfortunately, the link to welfare is not as simple as just measuring the degree of stereotypic behaviour: animals may show more stereotypies as a method of coping, or they may have acquired a stereotypy in a previous environment and are continuing to perform it (Mason & Latham, 2004). There are very few studies available on the prevalence of stereotypic behaviours in captive dolphins (for a review, see Clark, 2013); the predominant stereotypy reported is circular swimming, which has posed further problems since it is not clear whether the activity is indeed repetitive, invariant, and without function (Gygax, 1993; Sobel et al., 1994; Ugaz et al., 2013). More research into this topic is greatly needed. A measure of stereotypic behaviour was proposed in the C-Well<sup>®</sup> Assessment, but the thresholds for the acceptable, suboptimal, and poor welfare designations had to be adapted

from farm animal frequencies (Clegg et al., 2015). More research is also needed on negative affective states such as boredom and frustration which are also likely to be key correlates of understimulating environments and could be used to supplement measures of stereotypies (Mason et al., 2007; Burn, 2017). A study on zoo elephants found the odds of performing stereotypies increased by 26% for every 10% increase in time housed separately (Greco et al., 2017). Frustration and boredom in captive dolphins is barely discussed in the literature (Clark, 2013), and future work will have to use the few speculative indicators proposed (e.g., excessive anticipatory behaviour and tail slaps/side breaches; Clegg, 2017) and create experimental paradigms to test these.

*Anticipatory Behaviour*—The behaviour an animal performs in preparation for a predictable, upcoming event has been termed *anticipatory behaviour* (Spruijt et al., 2001). Animals from a range of taxa and cognitive abilities are able to anticipate predictable events due to the clear adaptive value, and researchers have found that, in general, anticipatory behaviour for a positive or negative event is differentiable (Moe et al., 2006; McGrath et al., 2016). Interestingly, anticipatory behaviour towards rewards specifically is thought to have a link with welfare. Although some level of anticipation for a positive event reflects positive emotions such as excitement, an excessive level of anticipation may reflect negative welfare states such as boredom and frustration due to the surrounding environment being understimulating (Spruijt et al., 2001; van der Harst & Spruijt, 2007; Watters, 2014). Studies on laboratory rats (*Rattus norvegicus*) have found initial support for the *reward-sensitivity theory* since individuals in more deprived, barren environments will perform more anticipatory behaviour before a food or social reward arrives (e.g., van den Berg et al., 1999; van der Harst et al., 2003; Makowska & Weary, 2016). The first studies on anticipatory behaviour in bottlenose dolphins have shown that behaviours such as spy-hopping and surface-looking were performed before training or shows during which the animals were fed (Jensen et al., 2013; Clegg et al., 2017c). Furthermore, a recent publication demonstrated that higher levels of anticipatory behaviour before training sessions in bottlenose dolphins were correlated to pessimistic judgement biases, indicating negative affective states and, therefore, agreeing with the reward-sensitivity theory (Clegg & Delfour, 2018). More research is clearly needed on this topic before anticipatory behaviour can be used as a welfare measure for dolphins or other species. However, it is also worth bearing in mind that just the anticipation of something positive, regardless of the consummation of the reward, can induce positive emotions (Gimsa et al., 2012; Opiol et al., 2015);

therefore, it is likely worth investigating anticipatory behaviour as a multifunctional welfare tool.

### *Cognitive Welfare Measures*

Returning to the Triangulation concept and what is thought to be the most accurate approach to measuring emotions, it is advantageous to apply cognitive measures when evaluating affective states or welfare (Harding et al., 2004; Webster, 2005). Understandably, cognitive measures are rarely included in practical welfare assessments since they are often either invasive in nature (e.g., measuring brain wave activity) and/or require a significant amount of time to train the animals (Paul et al., 2005). Fortunately, new techniques are being investigated that render it easier to assess the cognitive component of emotional responses; and while cognitive measures might not form part of assessments, they can still be used to validate other behavioural and physiological measures (Paul et al., 2005; Mendl et al., 2009).

The major development in this area over the last 10 years is certainly cognitive bias testing: human psychology paradigms have helped us to measure how cognitive processes are influenced by emotion in animals (Harding et al., 2004; Mendl et al., 2009). While there are several types of cognitive bias, the most common to be measured are judgement biases (decision making under ambiguity) through which numerous studies in a wide range of taxa have shown that animals in poorer welfare conditions judge more pessimistically, and those in better welfare conditions make more optimistic judgements (latest reviews by Baciadonna & McElligott, 2015; Roelofs et al., 2016). A judgement bias test was applied to marine mammals in a study on bottlenose dolphins in which it was found that dolphins who conducted more synchronous swimming outside of training sessions made more optimistic judgements in the test (Clegg et al., 2017a). The study was not able to conclude a causal relationship, but the results suggest that synchronous swimming, as a bond-affirming, affiliative behaviour (Connor et al., 2006b; Holobinko & Waring, 2010), may induce positive emotions or affective states in dolphins (Clegg et al., 2017a). This work is an example of how cognitive measurement of welfare, studied through taking the time to train the animals in a task, can be used to validate other (behavioural) welfare measures. While cognitive bias testing may seem like a technique only suited to captive research, it may in fact be possible in wild settings where the animals' natural preferences and aversions can be used (Brilot et al., 2009).

Another proposed cognitive measure of welfare is the lateralisation of brain function since it is thought that human and at least some animal brains may favour the left or right hemisphere to treat positively

or negatively connoted emotions, respectively (Rogers, 2002; Leliveld et al., 2013). The task now is to discover reliable ways to measure lateralities, which can manifest in many different forms and can vary inter-individually (Rogers, 2010). For example, the cetacean studies most relevant to the concept of emotional lateralisation have demonstrated that during nonthreatening situations, wild belugas and killer whales placed their calves on their right sides (i.e., information processed by the left hemisphere), with killer whales then moving the young to their left sides when the context became increasingly threatening (Karenina et al., 2010, 2013). Findings in other species also look promising: a link was recently shown between hand preference and cognitive bias in common marmosets (*Callithrix jacchus*; Gordon & Rogers, 2015); and during an experimental test, one male and one female California sea lion differentially used their flippers in a task with either negative versus positive conditions (Le Ray et al., 2017). However, more work is needed before measures of laterality can reliably indicate an individual's welfare.

### **What Are the Next Steps Towards Assessing Marine Mammal Welfare?**

Now that the existing research as well as some potential measures of marine mammal welfare have been outlined, we explore what the next directions for this field might be. While research is likely to initially progress on the most well-studied species (i.e., bottlenose dolphins) or in the more feasible experimental settings (i.e., in captive facilities), we argue that the time has come for multidimensional expertise regarding different marine mammal species to collaborate and start welfare discussions across many species. The recent, evident movement advocating for marine mammal welfare to be measured in captive settings (Ugaz et al., 2013; Brando et al., 2016; Clegg et al., 2017b), in the wild (Butterworth, 2017b; Papastavrou et al., 2017; Seuront & Cribb, 2017), and during rehabilitation (Petrauskas et al., 2006; Moore et al., 2007; Nicholson et al., 2007) should be addressed by scientists, industry stakeholders, and governments.

Those aiming to develop welfare assessments for marine mammals in any of the situations above should establish the methods *in situ* (Dawkins, 2006)—that is, using animal-based data—as it is very important to make sure the measures are valid and feasible for the animals in that particular environment. For captive studies, there is often the problem of small sample sizes, which may greatly limit statistical power and, thus, the ability to validate measures, so, where possible, interfacility collaborations should be established (e.g., as in

Miller et al., 2011; Dudzinski et al., 2012; Clegg et al., 2017c). Long-term collaborations should also be sought between the captive facilities and academics in the field, whether it be to establish graduate projects at the facility and/or to hire full-time ethologists or welfare scientists to conduct the research (Maple, 2007; Barber, 2009).

The remarkable propensity of captive marine mammals to learn tasks through positive reinforcement conditioning (Brando, 2010) should be exploited in research projects: further cognitive bias tasks, preference testing, and voluntary physiological sampling are all possible using such training. In the past, some facilities have shied away from conducting experimental studies on cognition as it was thought that isolation of the animals was necessary (I. Clegg, pers. obs., September 2015), but the recent cognitive bias tests were performed while the dolphins stayed in their group (Clegg et al., 2017a). In fact, this approach is being encouraged in research on other species (e.g., Malassis & Delfour, 2015) as a way to limit isolation stress from being separated (Roelofs et al., 2016), and it may also help us to develop new paradigms based on *situated* actions which could reveal different aspects of the animals' cognitive abilities (Delfour, 2015). Given that there are only a few validated welfare measures in existence for marine mammals, the first studies will find it the hardest. Similar to early animal welfare research, situations should be used when welfare is highly likely to be good or poor, and this applies to captive and wild welfare investigations. A study on welfare measures for belugas used this approach by taking data before and immediately after the animals were transported (Castellote & Fossa, 2006), and the fact that dolphins have been shown to perform less social play (Serres & Delfour, 2017) and had higher cortisol levels when noisy construction work was taking place in proximity (Monreal-Pawlowsky et al., 2017) also shows how supposed negative events can be used in welfare research (without being experimentally imposed).

As already emphasised, considering the welfare of a wild animal is just as valid as considering that of a captive animal, given that the concept describes a balance of positive and negative affective states. Furthermore, the increasing conflict between wild-life and humans, and the pressures placed on them to adapt to a changing environment, means that welfare evaluations would be beneficial in relevant decision-making processes (Paquet & Darimont, 2010; Papastavrou et al., 2017). Nevertheless, there are obviously limitations when working in the wild, chiefly access to and identification of the animals, which will mean that welfare assessments will be constructed differently to those for captive animals. To start, research could aim to develop measures

that are feasible above water and can be conducted in a relatively short time in case access to animals is restricted; a good example would be behavioural measures such as the frequency of synchronous swimming. This behaviour could be investigated in correlation with other measures to find out whether it might also be a sign of positive welfare or social support in wild bottlenose dolphins or in other delphinid species. Acoustic research and any welfare measures developed in relation to this (Castellote & Fossa, 2006) will also be very important in such settings for which noise pollution is becoming a serious threat to marine mammal welfare (Butterworth, 2017a). Research groups that have been conducting long-term studies on certain populations will be incredibly valuable for these first wild welfare studies since they often have the advantage of life history data, genetic information, and reliable identification of individuals (Wells, 2009). Support from regulatory bodies will also help greatly in expanding the focus to include behavioural and welfare aspects of conservation research, and it is very promising to see international bodies like the IWC looking to develop welfare assessments (Butterworth, 2017b).

Finally, the epistemology of science indicates that questions asked by scientists were, are, and always will be linked to or inspired by the society they live in. The rarefaction of basic resources such as land, energy, and water has already raised conflicts between humans and terrestrial animals, and the extent of our impact is now starting to be revealed for marine species (Butterworth, 2017a; Papastavrou et al., 2017). Measuring the welfare of marine and other animals still has a long way to progress and will be helped by other branches of science bringing with it new paradigms, theories, and concepts. Of course as ethologists, we believe that the behaviour of the animal will remain one of the keystones in assessing their welfare, but we acknowledge that we need to understand the animals' *umwelt*—their subjective perception of their environment—to effectively study, understand, and thus protect them (Delfour, 2010a, 2010b).

## Conclusion

Welfare science has evolved and now aims to assess how an animal is feeling by using objective, animal-based measures of both positive and negative states. Overall assessments of welfare have been developed for a few terrestrial species and generally include behavioural and physiological measures, with new approaches to conducting cognitive measures allowing another dimension of indicators to be identified. Past research on wild and captive marine mammals has largely been focussed on other topics than welfare, but there are many elements which can be used to suggest potential measures, and dedicated welfare

research for these taxa is slowly increasing. Initial studies have highlighted certain behavioural and physiological welfare indicators, demonstrated that cognitive tests are fruitful, and proposed a feasible protocol for a comprehensive welfare assessment. Research in captivity should build on these advances by collaborating among facilities and disciplines to design robust experiments with sufficient sample sizes. Amid calls for welfare science applications to wild marine mammals, a few projects have started theoretical discussions, and hopefully progress in this area will continue, perhaps capitalising on the wealth of knowledge acquired by long-term research programs. The objectives of this review were to first show that welfare assessment of marine mammals is indeed possible and that studies are already starting to be conducted to that effect; and second, that the holistic, multidimensional nature of welfare means that there are copious opportunities for existing marine mammal scientists to investigate aspects of welfare concurrently or, better yet, in collaborations.

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### Literature Cited

- Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., . . . Sapolsky, R. M. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, *43*(1), 67-82. [https://doi.org/10.1016/S0018-506X\(02\)00037-5](https://doi.org/10.1016/S0018-506X(02)00037-5)
- Animal Welfare Act (Laboratory Animal Welfare Act of 1966). Public Law 89-544, Animal Welfare Regulations: Subchapter A – Animal Welfare, 7 (1966).
- Atkinson, S., Crocker, D., Houser, D., & Mashburn, K. (2015). Stress physiology in marine mammals: How well do they fit the terrestrial model? *Journal of Comparative Physiology B*, *185*(5), 463-486. <https://doi.org/10.1007/s00360-015-0901-0>
- Azevedo, C. S., Cipreste, C. F., & Young, R. J. (2007). Environmental enrichment: A GAP analysis. *Applied Animal Behaviour Science*, *102*(3-4), 329-343. <https://doi.org/10.1016/j.applanim.2006.05.034>
- Bachmann, I., Bernasconi, P., Herrmann, R., Weishaupt, M. A., & Stauffacher, M. (2003). Behavioural and physiological responses to an acute stressor in crib-biting and control horses. *Applied Animal Behaviour Science*, *82*(4), 297-311. [https://doi.org/10.1016/S0168-1591\(03\)00086-8](https://doi.org/10.1016/S0168-1591(03)00086-8)
- Baciadonna, L., & McElligott, A. G. (2015). The use of judgement bias to assess welfare in farm livestock. *Animal Welfare*, *24*(1), 81-91. <https://doi.org/10.7120/09627286.24.1.081>
- Baird, B. A., Kuhar, C. W., Lukas, K. E., Amendolagine, L. A., Fuller, G. A., Nemet, J., . . . Schook, M. W. (2016). Program animal welfare: Using behavioral and physiological measures to assess the well-being of animals used for education programs in zoos. *Applied Animal Behaviour Science*, *176*, 150-162. <https://doi.org/10.1016/j.applanim.2015.12.004>
- Barber, J. C. E. (2009). Programmatic approaches to assessing and improving animal welfare in zoos and aquariums. *Zoo Biology*, *28*(6), 519-530. <https://doi.org/10.1002/zoo.20260>
- Barnard, S., & Ferri, N. (2015). Development of a new welfare assessment protocol for practical application in long-term dog shelters. *Veterinary Record*, *178*, 1-8. <https://doi.org/10.1136/vr.103336>
- Bateson, P. (2014). Play, playfulness, creativity and innovation. *Animal Behavior and Cognition*, *1*(2), 99-112. <https://doi.org/10.12966/abc.05.02.2014>
- Bechshoft, T., Sonne, C., Dietz, R., Born, E., Novak, M., Henchey, E., & Meyer, J. (2012). Cortisol levels in hair of East Greenland polar bears. *Science of the Total Environment*, *409*(4), 831-834. <https://doi.org/10.1016/j.scitotenv.2010.10.047>
- Berglund, M. (2005). *Acoustic enrichment for dolphins in pool environment* (Master's thesis). Linköping University, Linköping, Sweden.
- Biancani, B., Dalt, L. D., Gallina, G., Capolongo, F., & Gabai, G. (2017). Fecal cortisol radioimmunoassay to monitor adrenal gland activity in the bottlenose dolphin (*Tursiops truncatus*) under human care. *Marine Mammal Science*, *33*(4), 1014-1034. <https://doi.org/10.1111/mms.12424>
- Blokhuis, H. J. (2008). International cooperation in animal welfare: The Welfare Quality® project. *Acta Veterinaria Scandinavica*, *50*(Suppl. 1), S10. <https://doi.org/10.1186/1751-0147-50-S1-S10>
- Blokhuis, H. J., Veissier, I., Miele, M., & Jones, B. (2010). The Welfare Quality® project and beyond: Safeguarding farm animal well-being. *Acta Agriculturae Scandinavica, Section A*, *60*(September), 129-140. <https://doi.org/10.1080/09064702.2010.523480>
- Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., . . . Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology and Behavior*, *92*(3), 375-397. <https://doi.org/10.1016/j.physbeh.2007.02.003>
- Botreau, R., Gaborit, M., & Veissier, I. (2012). Applying Welfare Quality® strategy to design a welfare assessment tool for foxes and mink farms. In *Proceedings of the Xth International Scientific Congress in Fur Animal Production* (pp. 460-468). Wageningen, The Netherlands: Wageningen Academic Publishers. [https://doi.org/10.3920/978-90-8686-760-8\\_67](https://doi.org/10.3920/978-90-8686-760-8_67)
- Botreau, R., Veissier, I., Butterworth, A., Bracke, M. B. M., & Keeling, L. J. (2007). Definition of criteria for overall assessment of animal welfare. *Animal Welfare*, *16*(2), 225-228.
- Botreau, R., Bonde, M., Butterworth, A., Perny, P., Bracke, M. B. M., Capdeville, J., & Veissier, I. (2007).

- Aggregation of measures to produce an overall assessment of animal welfare. Part 1: A review of existing methods. *Animal*, 1(8), 1179-1187. <https://doi.org/10.1017/S1751731107000535>
- Bracke, M. B. M., Spruijt, B. M., & Metz, J. H. M. (1999). Overall animal welfare assessment reviewed. Part 1: Is it possible? *Netherlands Journal of Agricultural Science*, 47, 279-291.
- Brando, S. I. C. A. (2010). Advances in husbandry training in marine mammal care programs. *International Journal of Comparative Psychology*, 23, 777-791. <https://doi.org/10.1016/j.jebdp.2005.01.008>
- Brando, S. I. C. A., Bowles, A. E., Böye, M., Dudzinski, K. M., van Elk, N., Lucke, K., . . . Wahlberg, M. (2016). Proceedings of marine mammal welfare workshops hosted in the Netherlands and the USA in 2012. *Aquatic Mammals*, 42(3), 392-416. <https://doi.org/10.1578/AM.42.3.2016.392>
- Brilot, B. O., Normandale, C. L., Parkin, A., & Bateson, M. (2009). Can we use starlings' aversion to eyespots as the basis for a novel "cognitive bias" task? *Applied Animal Behaviour Science*, 118(3-4), 182-190. <https://doi.org/10.1016/j.applanim.2009.02.015>
- Broom, D. M. (1991). Animal welfare: Concepts and measurement. *Journal of Animal Science*, 69(10), 4167-4175. <https://doi.org/10.2527/1991.69104167x>
- Broom, D. M., & Fraser, A. F. (2015). *Domestic animal behaviour and welfare* (5th ed.). Oxfordshire, UK: CABI Publishing.
- Broom, D. M., & Johnson, K. G. (1993). *Stress and animal welfare*. Dordrecht: Springer Netherlands.
- Burn, C. C. (2017). Bestial boredom: A biological perspective on animal boredom and suggestions for its scientific investigation. *Animal Behaviour*, 130, 1-43. <https://doi.org/10.1016/j.anbehav.2017.06.006>
- Butterworth, A. (Ed.). (2017a). *Marine mammal welfare: Human induced change in the marine environment and its impacts on marine mammal welfare*. Cham, Switzerland: Springer Nature.
- Butterworth, A. (2017b). *Report of the Workshop to Support the IWC's Consideration of Non-Hunting Related Aspects of Cetacean Welfare* (IWC/66/WKM&WI Report 01). Cambridge, UK: International Whaling Commission.
- Butterworth, A., Clegg, I. L. K., & Bass, C. (2012). *Untangled. Marine debris: A global picture of the impact on animal welfare and of animal-focused solutions*. London: World Society for the Protection of Animals.
- Carlstead, K., Brown, J. L., & Strawn, W. (1993). Behavioral and physiological correlates of stress in laboratory cats. *Applied Animal Behaviour Science*, 38(2), 143-158. [https://doi.org/10.1016/0168-1591\(93\)90062-T](https://doi.org/10.1016/0168-1591(93)90062-T)
- Castellote, M., & Fossa, F. (2006). Measuring acoustic activity as a method to evaluate welfare in captive beluga whales (*Delphinapterus leucas*). *Aquatic Mammals*, 32(3), 325-333. <https://doi.org/10.1578/AM.32.3.2006.325>
- Christiansen, F., & Lusseau, D. (2015). Linking behavior to vital rates to measure the effects of non-lethal disturbance on wildlife. *Conservation Letters*, 8(6), 424-431. <https://doi.org/10.1111/conl.12166>
- Clark, F. E. (2013). Marine mammal cognition and captive care: A proposal for cognitive enrichment in zoos and aquariums. *Journal of Zoo and Aquarium Research*, 1(1), 1-6. <https://doi.org/https://doi.org/10.19227/jzar.v1i1.19>
- Clark, F. E., Davies, S. L., Madigan, A. W., Warner, A. J., & Kuczaj II, S. A. (2013). Cognitive enrichment for bottlenose dolphins (*Tursiops truncatus*): Evaluation of a novel underwater maze device. *Zoo Biology*, 32(6), 608-619. <https://doi.org/10.1002/zoo.21096>
- Clegg, I. L. K. (2017). *Developing welfare parameters for bottlenose dolphins (Tursiops truncatus) under human care* (Doctoral dissertation). Université Paris, Paris, France. 217 pp.
- Clegg, I. L. K., & Butterworth, A. (2017a). Assessing the welfare of Cetacea. In A. Butterworth (Ed.), *Marine mammal welfare: Human induced change in the marine environment and its impacts on marine mammal welfare* (pp. 183-214). Cham, Switzerland: Springer Nature.
- Clegg, I. L. K., & Butterworth, A. (2017b). Assessing the welfare of pinnipeds. In A. Butterworth (Ed.), *Marine mammal welfare: Human induced change in the marine environment and its impacts on marine mammal welfare* (pp. 273-298). Cham, Switzerland: Springer Nature.
- Clegg, I. L. K., & Delfour, F. (2018). Cognitive judgement bias is associated with frequency of anticipatory behaviour in bottlenose dolphins. *Zoo Biology*. Early view. <https://doi.org/10.1002/zoo.21400>
- Clegg, I. L. K., Borger-Turner, J. L., & Eskelinen, H. C. (2015). C-Well: The development of a welfare assessment index for captive bottlenose dolphins (*Tursiops truncatus*). *Animal Welfare*, 24(3), 267-282. <https://doi.org/10.7120/09627286.24.3.267>
- Clegg, I. L. K., Rödel, H. G., & Delfour, F. (2017a). Bottlenose dolphins engaging in more social affiliative behaviour judge ambiguous cues more optimistically. *Behavioural Brain Research*, 322, 115-122. <https://doi.org/10.1016/j.bbr.2017.01.026>
- Clegg, I. L. K., van Elk, C. E., & Delfour, F. (2017b). Applying welfare science to bottlenose dolphins (*Tursiops truncatus*). *Animal Welfare*, 26(2), 165-176. <https://doi.org/10.7120/09627286.26.2.165>
- Clegg, I. L. K., Rödel, H. G., Boivin, X., & Delfour, F. (2018). Looking forward to interacting with their caretakers: Dolphins' anticipatory behaviour indicates their motivation to participate in specific events. *Applied Animal Behaviour Science*. Early view. <https://doi.org/10.1016/j.applanim.2018.01.015>
- Clegg, I. L. K., Rödel, H. G., Cellier, M., Vink, D., Michaud, I., Mercera, B., . . . Delfour, F. (2017c). Schedule of human-controlled periods structures bottlenose dolphin (*Tursiops truncatus*) behavior in their free-time. *Journal of Comparative Psychology*, 131(3), 214-224. <https://doi.org/10.1037/com0000059>
- Connor, R., Mann, J., & Watson-Capps, J. (2006a). A sex-specific affiliative contact behavior in Indian Ocean bottlenose dolphins, *Tursiops* sp. *Ethology*, 112(7), 631-638. <https://doi.org/10.1111/j.1439-0310.2006.01203.x>

- Connor, R. C., Smolker, R., & Bejder, L. (2006b). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour*, 72(6), 1371-1378. <https://doi.org/10.1016/j.anbehav.2006.03.014>
- Coulon, M., Nowak, R., Peyrat, J., Chandèze, H., Boissy, A., & Boivin, X. (2015). Do lambs perceive regular human stroking as pleasant? Behavior and heart rate variability analyses. *PLOS ONE*, 10(2), e0118617. <https://doi.org/10.1371/journal.pone.0118617>
- Dawkins, M. S. (1980). *Animal suffering: The science of animal welfare*. London: Chapman & Hall.
- Dawkins, M. S. (1998). Evolution and animal welfare. *The Quarterly Review of Biology*, 73(3), 305-328. Retrieved from [www.jstor.org/stable/3036918](http://www.jstor.org/stable/3036918)
- Dawkins, M. S. (2006). A user's guide to animal welfare science. *Trends in Ecology and Evolution*, 21(2), 77-82. <https://doi.org/10.1016/j.tree.2005.10.017>
- Dawkins, M. S. (2015). Animal welfare and the paradox of animal consciousness. *Advances in the Study of Behavior*, 47, 5-38. <https://doi.org/10.1016/bs.asb.2014.11.001>
- De Passillé, A. M., & Rushen, J. (2005). Can we measure human-animal interactions in on-farm animal welfare assessment? Some unresolved issues. *Applied Animal Behaviour Science*, 92(3), 193-209. <https://doi.org/10.1016/j.applanim.2005.05.006>
- Delfour, F. (2010a). Conscience, souffrance et bien-être de l'animal-sujet (Consciousness, suffering and well-being of the animal-subject). In P. Jouventin (Ed.), *La raison des plus forts* (The reason of the strongest) (pp. 123-147). Paris: Editions IMHO.
- Delfour, F. (2010b). Marine mammals enact individual worlds. *International Journal of Comparative Psychology*, 23, 792-810. <https://doi.org/10.1016/j.jebdp.2005.01.005>
- Delfour, F. (2015). Contrepoint: L'éthologie constructiviste des relations anthro-canines (Counterpoint: The constructivist ethology of anthro-canine relations). In V. Servais (Ed.), *Sociabilités humaines et sociabilités canines: Médiations épistémologiques* (Human sociability and canine sociability: Epistemological mediations) (pp. 75-91). Lormont, France: Le Bord de L'Eau.
- Delfour, F., & Beyer, H. (2012). Assessing the effectiveness of environmental enrichment in bottlenose dolphins (*Tursiops truncatus*). *Zoo Biology*, 31(2), 137-150. <https://doi.org/10.1002/zoo.20383>
- Delfour, F., Faulkner, C., & Carter, T. (2017). Object manipulation and play behaviour in bottlenose dolphins (*Tursiops truncatus*) under human care. *International Journal of Comparative Psychology*, 30, 1-21.
- Désiré, L., Boissy, A., & Veissier, I. (2002). Emotions in farm animals: A new approach to animal welfare in applied ethology. *Behavioural Processes*, 60(2), 165-180. [https://doi.org/10.1016/S0376-6357\(02\)00081-5](https://doi.org/10.1016/S0376-6357(02)00081-5)
- Draper, C., & Harris, S. (2012). The assessment of animal welfare in British zoos by government-appointed inspectors. *Animals*, 2(4), 507-528. <https://doi.org/10.3390/ani2040507>
- Dudzinski, K. M. (2010). Overlap between information gained from complementary and comparative studies of captive and wild dolphins. *International Journal of Comparative Psychology*, 23(2), 566-586. <https://doi.org/10.1016/j.jebdp.2005.04.004>
- Dudzinski, K. M., & Ribic, C. A. (2017). Pectoral fin contact as a mechanism for social bonding among dolphins. *Animal Behavior and Cognition*, 4(1), 30-48. <https://doi.org/10.12966/abc.03.02.2017>
- Dudzinski, K. M., Gregg, J., Melillo-Sweeting, K., Seay, B., Levensgood, A., & Kuczaj II, S. A. (2012). Tactile contact exchanges between dolphins: Self-rubbing versus inter-individual contact in three species from three geographies. *International Journal of Comparative Psychology*, 25, 21-43.
- Dunn, J. L., Buck, J. D., & Robeck, T. R. (2001). Bacterial diseases of cetaceans and pinnipeds. In L. A. Dierauf & F. M. D. Gulland (Eds.), *CRC handbook of marine mammal medicine* (2nd ed., pp. 309-336). Boca Raton, FL: CRC Press.
- EC Council Directive. (1999). *Council Directive 1999/22/EC relating to the keeping of wild animals in zoos*.
- Fair, P. A., Schaefer, A. M., Romano, T. A., Bossart, G. D., Lamb, S. V., & Reif, J. S. (2014). Stress response of wild bottlenose dolphins (*Tursiops truncatus*) during capture-release health assessment studies. *General and Comparative Endocrinology*, 206(July), 203-212. <https://doi.org/10.1016/j.ygcen.2014.07.002>
- Farm Animal Welfare Council (FAWC). (1992). Farm Animal Welfare Council (FAWC) updates the Five Freedoms. *Veterinary Record*, 17, 357.
- Fraser, D., Weary, D. M., Pajor, E. A., & Milligan, B. N. (1997). A scientific conception of animal welfare that reflects ethical concerns. *Animal Welfare*, 6(2), 187-205.
- Frohoff, T. G., & Packard, J. M. (1995). Human interactions with free-ranging and captive bottlenose dolphins. *Anthrozoos: A Multidisciplinary Journal of the Interactions of People & Animals*, 8(1), 44-53. <https://doi.org/10.2752/089279395787156527>
- Galhardo, L., Appleby, M. C., Waran, N. K., & dos Santos, M. E. (1996). Spontaneous activities of captive performing bottlenose dolphins (*Tursiops truncatus*). *Animal Welfare*, 5(4), 373-389.
- Gimsa, U., Kloeckner, P., Jaskulke, S., Kanitz, E., Tuchscherer, M., Schoen, P. C., . . . Manteuffel, G. (2012). Does anticipation induce affective states with consequences for immunocompetence? *Brain, Behavior, and Immunity*, 26, S12-S13. <https://doi.org/http://dx.doi.org/10.1016/j.bbi.2012.07.068>
- Gonyou, H. W. (1994). Why the study of animal behavior is associated with the animal welfare issue. *Journal of Animal Science*, 72(8), 2171-2177.
- Gordon, D. J., & Rogers, L. J. (2015). Cognitive bias, hand preference and welfare of common marmosets. *Behavioural Brain Research*, 287, 100-108. <https://doi.org/10.1016/j.bbr.2015.03.037>
- Greco, B. J., Meehan, C. L., Heinsius, J. L., & Mench, J. A. (2017). Why pace? The influence of social, housing,

- management, life history, and demographic characteristics on locomotor stereotypy in zoo elephants. *Applied Animal Behaviour Science*, 194, 104-111. <https://doi.org/10.1016/j.applanim.2017.05.003>
- Greene, W. E., Melillo-Sweeting, K., & Dudzinski, K. M. (2011). Comparing object play in captive and wild dolphins. *International Journal of Comparative Psychology*, 24(3), 292-306. <https://doi.org/10.5811/westjem.2011.5.6700>
- Grindrod, J. A. E., & Cleaver, J. A. (2001). Environmental enrichment reduces the performance of stereotypic circling behaviour in captive common seals (*Phoca vitulina*). *Animal Welfare*, 10(1), 53-63.
- Gygax, L. (1993). Spatial movement patterns and behaviour of two captive bottlenose dolphins (*Tursiops truncatus*): Absence of stereotyped behaviour or lack of definition? *Applied Animal Behaviour Science*, 38(3-4), 337-344. [https://doi.org/10.1016/0168-1591\(93\)90031-J](https://doi.org/10.1016/0168-1591(93)90031-J)
- Harding, E. J., Paul, E. S., & Mendl, M. (2004). Cognitive bias and affective state. *Nature*, 427(January), 312. <https://doi.org/10.1038/427312a>
- Hart, L. B., Wells, R. S., & Schwacke, L. H. (2013). Reference ranges for body condition in wild bottlenose dolphins *Tursiops truncatus*. *Aquatic Biology*, 18(1), 63-68. <https://doi.org/10.3354/ab00491>
- Harvey, B. S., Dudzinski, K. M., & Kuczaj II, S. A. (2017). Associations and the role of affiliative, agonistic, and socio-sexual behaviors among common bottlenose dolphins (*Tursiops truncatus*). *Behavioural Processes*, 135, 145-156. <https://doi.org/10.1016/j.beproc.2016.12.013>
- Hekman, J. P., Karas, A. Z., & Dreschel, N. A. (2012). Salivary cortisol concentrations and behavior in a population of healthy dogs hospitalized for elective procedures. *Applied Animal Behaviour Science*, 141(3-4), 149-157. <https://doi.org/10.1016/j.applanim.2012.08.007>
- Held, S. D. E., & Špinko, M. (2011). Animal play and animal welfare. *Animal Behaviour*, 81(5), 891-899. <https://doi.org/10.1016/j.anbehav.2011.01.007>
- Hemsworth, P. H. (2007). Ethical stockmanship. *Australian Veterinary Journal*, 85(5), 194-200. <https://doi.org/10.1111/j.1751-0813.2007.00112.x>
- Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals*, 22(2), 61-79.
- Herzing, D. L. (2000). Acoustics and social behavior of wild dolphins: Implications for a sound society. In W. W. L. Au & R. Fay (Eds.), *Hearing by whales and dolphins* (pp. 225-272). New York: Springer.
- Herzing, D. L., & Johnson, C. M. (1997). Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985-1995. *Aquatic Mammals*, 29(3), 335-341.
- Hill, H., & Lackups, M. (2010). Journal publication trends regarding cetaceans found in both wild and captive environments: What do we study and where do we publish? *International Journal of Comparative Psychology*, 23, 414-534.
- Hill, H., & Ramirez, D. (2014). Adults play but not like their young: The frequency and types of play by belugas (*Delphinapterus leucas*) in human care. *Animal Behavior and Cognition*, 1(2), 166-185. <https://doi.org/10.12966/abc.05.07.2014>
- Hill, H., Guarino, S., Dietrich, S., & St. Leger, J. (2016). An inventory of peer-reviewed articles on killer whales (*Orcinus orca*) with a comparison to bottlenose dolphins (*Tursiops truncatus*). *Animal Behavior and Cognition*, 3(3), 135-149. <https://doi.org/10.12966/abc.03.08.2016>
- Hocking, D. P., Salverson, M., & Evans, A. R. (2015). Foraging-based enrichment promotes more varied behaviour in captive Australian fur seals (*Arctocephalus pusillus doriferus*). *PLOS ONE*, 10(5). <https://doi.org/10.1371/journal.pone.0124615>
- Holobinko, A., & Waring, G. H. (2010). Conflict and reconciliation behavior trends of the bottlenose dolphin (*Tursiops truncatus*). *Zoo Biology*, 29(5), 567-585. <https://doi.org/10.1002/zoo.20293>
- Hopster, H., & de Jong, I. (2014). *Welfare of sea lions in travelling circuses*. Lelystad, The Netherlands: Wageningen UR Livestock Research.
- Hosey, G., & Melfi, V. (2014). Human-animal interactions, relationships and bonds: A review and analysis of the literature. *International Journal of Comparative Psychology*, 27(1), 117-142. <https://doi.org/10.5811/westjem.2011.5.6700>
- Hoy, J. M., Murray, P. J., & Tribe, A. (2010). Thirty years later: Enrichment practices for captive mammals. *Zoo Biology*, 29(3), 303-316. <https://doi.org/10.1002/zoo.20254>
- Innes, W., DeMaster, D., Rodriguez, A., & Crowder, L. (2005). Survival rates of marine mammals in captivity: Temporal trends and institutional analysis. *Sixteenth Biennial Conference on the Biology of Marine Mammals*, San Diego, CA. 136 pp.
- Janik, V. M., & Thompson, P. M. (1996). Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. *Marine Mammal Science*, 12(4), 597-602. <https://doi.org/10.1111/j.1748-7692.1996.tb00073.x>
- Jensen, A-L. M., Delfour, F., & Carter, T. (2013). Anticipatory behavior in captive bottlenose dolphins (*Tursiops truncatus*): A preliminary study. *Zoo Biology*, 32(4), 436-444. <https://doi.org/10.1002/zoo.21077>
- Jiang, Y., Lück, M., & Parsons, E. C. M. (2007). Public awareness, education, and marine mammals in captivity. *Tourism Review International*, 11(3), 237-249. <https://doi.org/10.3727/154427207783948829>
- Joblon, M. J., Pokras, M. A., Morse, B., Harry, C. T., Rose, K. S., Sharp, S. M., . . . Moore, M. J. (2014). Body condition scoring system for delphinids based on short-beaked common dolphins (*Delphinus delphis*). *Journal of Marine Animals and Their Ecology*, 7(2), 5-13.
- Joseph, B., & Antrim, J. (2010). Special considerations for the maintenance of marine mammals in captivity. In M. McPhee & K. Carlstead (Eds.), *Wild mammals in captivity: Principles and techniques for zoo management* (pp. 181-216). Chicago: The University of Chicago Press.

- Kagan, R., Carter, S., & Allard, S. (2015, May). A universal animal welfare framework for zoos. *Journal of Applied Animal Welfare Science*, *18*(Supp. 1), S1-S10. <https://doi.org/10.1080/10888705.2015.1075830>
- Karenina, K., Giljov, A., Ivkovich, T., Burdin, A., & Malashichev, Y. (2013). Lateralization of spatial relationships between wild mother and infant orcas, *Orcinus orca*. *Animal Behaviour*, *86*(6), 1225-1231. <https://doi.org/10.1016/j.anbehav.2013.09.025>
- Karenina, K., Giljov, A., Baranov, V., Osipova, L., Krasnova, V., & Malashichev, Y. (2010). Visual laterality of calf-mother interactions in wild whales. *PLOS ONE*, *5*(11), e13787. <https://doi.org/10.1371/journal.pone.0013787>
- Kastelein, R. A., & Wiepkema, P. R. (1988). The significance of training for the behaviour of Stellar sea lions in human care. *Aquatic Mammals*, *14*(1), 39-41.
- Kastelein, R. A., & Wiepkema, P. R. (1989). A digging trough as occupational therapy for Pacific walrus (*Odobenus rosmarus divergens*) in human care. *Aquatic Mammals*, *15*(1), 9-17.
- Kirkwood, J. K., Sainsbury, A. W., & Bennett, P. M. (1994). The welfare of free-living wild animals: Methods of assessment. *Animal Welfare*, *3*(4), 257-273.
- Krajnauk, E. (1996). Floating beaching platform for bottlenose dolphins. *Shape Enrichment*, *5*, 7.
- Kuczaj II, S. A., & Eskelinen, H. C. (2014). Why do dolphins play? *Animal Behavior and Cognition*, *1*(2), 113-127. <https://doi.org/10.12966/abc.05.03.2014>
- Kuczaj II, S. A., Highfill, L. E., Makecha, R. N., & Byerly, H. C. (2013). Why do dolphins smile? A comparative perspective on dolphin emotions and emotional expressions. In S. Watanabe & S. A. Kuczaj II (Eds.), *Emotions of animals and humans* (pp. 63-85). Tokyo: Springer.
- Kuczaj II, S. A., Lacinak, T., Otto, F., Trone, M., Solangi, M., & Ramos, J. (2002). Keeping environmental enrichment enriching. *International Journal of Comparative Psychology*, *15*(2), 127-137.
- Kyngdon, D. J., Minot, E. O., & Stafford, K. J. (2003). Behavioural responses of captive common dolphins *Delphinus delphis* to a "Swim-with-Dolphin" programme. *Applied Animal Behaviour Science*, *81*(2), 163-170. [https://doi.org/10.1016/S0168-1591\(02\)00255-1](https://doi.org/10.1016/S0168-1591(02)00255-1)
- Le Ray, S., Le Gal, M., & Delfour, F. (2017). Does emotional state influence motor lateralization in California sea lions (*Zalophus californianus*)? *Acta Ethologica*, *20*(3), 279-289. <https://doi.org/10.1007/s10211-017-0273-4>
- Leliveld, L. M. C., Langbein, J., & Puppe, B. (2013). The emergence of emotional lateralization: Evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science*, *145*(1-2), 1-14. <https://doi.org/10.1016/j.applanim.2013.02.002>
- Leliveld, L. M. C., Döpjan, S., Tuchscherer, A., & Puppe, B. (2016). Behavioural and physiological measures indicate subtle variations in the emotional valence of young pigs. *Physiology and Behavior*, *157*, 116-124. <https://doi.org/10.1016/j.physbeh.2016.02.002>
- Makowska, I. J., & Weary, D. M. (2016). Differences in anticipatory behaviour between rats (*Rattus norvegicus*) housed in standard versus semi-naturalistic laboratory environments. *PLOS ONE*, *11*(1). <https://doi.org/10.1371/journal.pone.0147595>
- Malassis, R., & Delfour, F. (2015). Sea lions' (*Zalophus californianus*) use of human pointing gestures as referential cues. *Learning & Behavior*, *43*, 101-112. <https://doi.org/10.3758/s13420-014-0165-7>
- Maple, T. L. (2007). Toward a science of welfare for animals in the zoo. *Journal of Applied Animal Welfare Science*, *10*(1), 63-70. <https://doi.org/10.1080/10888700701277659>
- Marley, S. A., Cheney, B., & Thompson, P. M. (2013). Using tooth rakes to monitor population and sex differences in aggressive behaviour in bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, *39*(2), 107-115. <https://doi.org/10.1578/AM.39.2.2013.107>
- Mason, G., & Latham, N. R. (2004). Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Animal Welfare*, *13*(Supp.), 57-69.
- Mason, G., & Rushen, J. (2006). A decade-or-more's progress in understanding stereotypic behaviour. In G. Mason & J. Rushen (Eds.), *Stereotypic animal behaviour: Fundamentals and applications to welfare* (2nd ed., pp. 1-18). Oxfordshire, UK: CABI Publishing.
- Mason, G., & Veasey, J. S. (2010). How should the psychological well-being of zoo elephants be objectively investigated? *Zoo Biology*, *29*(2), 237-255. <https://doi.org/10.1002/zoo.20256>
- Mason, G., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science*, *102*(3-4), 163-188. <https://doi.org/10.1016/j.applanim.2006.05.041>
- McCowan, B., Marino, L., Vance, E., Walke, L., & Reiss, D. (2000). Bubble ring play of bottlenose dolphins (*Tursiops truncatus*): Implications for cognition. *Journal of Comparative Psychology*, *114*(1), 98-106. <https://doi.org/10.1037/0735-7036.114.1.98>
- McGrath, N., Burman, O., Dwyer, C., & Phillips, C. J. C. (2016). Does the anticipatory behaviour of chickens communicate reward quality? *Applied Animal Behaviour Science*, *184*, 80-90. <https://doi.org/10.1016/j.applanim.2016.08.010>
- Mellor, D. J. (2016). Updating animal welfare thinking: Moving beyond the "Five Freedoms" towards "A Life Worth Living." *Animals*, *6*(21), 1-20. <https://doi.org/10.3390/ani6030021>
- Mellor, D. J., & Beausoleil, N. (2015). Extending the "Five Domains" model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare*, *24*(3), 241-253. <https://doi.org/10.7120/09627286.24.3.241>
- Mellor, D. J., & Reid, C. S. W. (1994). Concepts of animal well-being and predicting the impact of procedures on experimental animals. In R. Baker, G. Jenkin, & D. Mellor (Eds.), *Improving the well-being of animals in the research environment* (pp. 3-18). Adelaide,



- Australia: Australian and New Zealand Council for the Care of Animals in Research and Teaching.
- Menargues, A., Urios, V., & Mauri, M. (2008). Welfare assessment of captive Asian elephants (*Elephas maximus*) and Indian rhinoceros (*Rhinoceros unicornis*) using salivary cortisol measurement. *Animal Welfare*, *17*(3), 305-312.
- Mendl, M., Burman, O. H. P., & Paul, E. S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1696), 2895-2904. <https://doi.org/10.1098/rspb.2010.0303>
- Mendl, M., Burman, O., Parker, R. M. A., & Paul, E. S. (2009). Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science*, *118*(3-4), 161-181. <https://doi.org/10.1016/j.applanim.2009.02.023>
- Miller, D. L., Ewing, R. Y., & Bossart, G. D. (2001). Emerging and resurging diseases. In L. A. Dierauf & F. M. D. Gulland (Eds.), *CRC handbook of marine mammal medicine* (2nd ed., pp. 15-30). Boca Raton, FL: CRC Press. <https://doi.org/10.2307/302397>
- Miller, L. J., Mellen, J., Greer, T., & Kuczaj II, S. A. (2011). The effects of education programmes on Atlantic bottlenose dolphin (*Tursiops truncatus*) behaviour. *Animal Welfare*, *20*, 159-172.
- Millman, S. T. (2007). Sickness behaviour and its relevance to animal welfare assessment at the group level. *Animal Welfare*, *16*(2), 123-125.
- Moe, R. O., Bakken, M., Kittilsen, S., Kingsley-Smith, H., & Spruijt, B. M. (2006). A note on reward-related behaviour and emotional expressions in farmed silver foxes (*Vulpes vulpes*): Basis for a novel tool to study animal welfare. *Applied Animal Behaviour Science*, *101*(3-4), 362-368. <https://doi.org/10.1016/j.applanim.2006.02.004>
- Mononen, J., Møller, S. H., Hansen, S. W., Hovland, A. L., Koistinen, T., Lidfors, L., . . . Ahola, L. (2012). The development of on-farm welfare assessment protocols for foxes and mink: The WelFur project. *Animal Welfare*, *21*(3), 363-371. <https://doi.org/10.7120/09627286.21.3.363>
- Monreal-Pawłowski, T., Carbajal, A., Tallo-Parra, O., Sabés-Alsina, M., Monclús, L., Almunia, J., . . . Lopez-Bejar, M. (2017). Daily salivary cortisol levels in response to stress factors in captive common bottlenose dolphins (*Tursiops truncatus*): A potential welfare indicator. *Veterinary Record*, *180*(24), 593.
- Moore, M., Early, G., Touhey, K., Barco, S., Gulland, F. M. D., & Wells, R. S. (2007). Rehabilitation and release of marine mammals in the United States: Risks and benefits. *Marine Mammal Science*, *23*(4), 731-750. <https://doi.org/10.1111/j.1748-7692.2007.00146.x>
- Newberry, R. C. (1995). Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science*, *44*(2-4), 229-243. [https://doi.org/10.1016/0168-1591\(95\)00616-Z](https://doi.org/10.1016/0168-1591(95)00616-Z)
- Nicholson, T. E., Mayer, K. A., Staedler, M. M., & Johnson, A. B. (2007). Effects of rearing methods on survival of released free-ranging juvenile southern sea otters. *Biological Conservation*, *138*(3-4), 313-320. <https://doi.org/10.1016/j.biocon.2007.04.026>
- Nowacek, S. M., & Wells, R. S. (2001). Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, *17*(4), 673-688. <https://doi.org/doi:10.1111/j.1748-7692.2001.tb01292.x>
- Opiol, H., Pavlovski, I., Michalik, M., & Mistlberger, R. E. (2015). Ultrasonic vocalizations in rats anticipating circadian feeding schedules. *Behavioural Brain Research*, *284*, 42-50. <https://doi.org/10.1016/j.bbr.2015.02.003>
- Ortiz, R. M., & Worthy, G. A. J. (2000). Effects of capture on adrenal steroid and vasopressin concentrations in free-ranging bottlenose dolphins (*Tursiops truncatus*). *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *125*(3), 317-324. [https://doi.org/10.1016/S1095-6433\(00\)00158-6](https://doi.org/10.1016/S1095-6433(00)00158-6)
- Pack, A. A., & Herman, L. M. (2006). Dolphin social cognition and joint attention: Our current understanding. *Aquatic Mammals*, *32*(4), 443-460. <https://doi.org/10.1578/AM.32.4.2006.443>
- Palme, R. (2012). Monitoring stress hormone metabolites as a useful, non-invasive tool for welfare assessment in farm animals. *Animal Welfare*, *21*, 331-337. <https://doi.org/10.7120/09627286.21.3.331>
- Papastavrou, V., Leaper, R., & Lavigne, D. (2017). Why management decisions involving marine mammals should include animal welfare. *Marine Policy*, *79*(October 2016), 19-24. <https://doi.org/10.1016/j.marpol.2017.02.001>
- Papciak, J., Popik, P., Fuchs, E., & Rygula, R. (2013). Chronic psychosocial stress makes rats more "pessimistic" in the ambiguous-cue interpretation paradigm. *Behavioural Brain Research*, *256*, 305-310. <https://doi.org/10.1016/j.bbr.2013.08.036>
- Paquet, P. C., & Darimont, C. T. (2010). Wildlife conservation and animal welfare: Two sides of the same coin? *Animal Welfare*, *19*, 177-190.
- Paul, E. S., Harding, E. J., & Mendl, M. (2005). Measuring emotional processes in animals: The utility of a cognitive approach. *Neuroscience and Biobehavioral Reviews*, *29*(3), 469-491. <https://doi.org/10.1016/j.neubiorev.2005.01.002>
- Paulos, R. D., Trone, M., & Kuczaj II, S. A. (2010). Play in wild and captive cetaceans. *International Journal of Comparative Psychology*, *23*(4), 701-722. <https://doi.org/10.1016/j.socscimed.2010.01.002>
- Pedernera-Romano, C., Valdez, R. A., Singh, S., Chiappa, X., Romano, M. C., & Galindo, F. (2006). Salivary cortisol in captive dolphins (*Tursiops truncatus*): A non-invasive technique. *Animal Welfare*, *15*(4), 359-362.
- Perelberg, A., & Schuster, R. (2009). Bottlenose dolphins (*Tursiops truncatus*) prefer to cooperate when petted: Integrating proximate and ultimate explanations II. *Journal of Comparative Psychology*, *123*(1), 45-55. <https://doi.org/10.1037/a0013585>
- Petrauskas, L., Tuomi, P., & Atkinson, S. (2006). Non-invasive monitoring of stress hormone levels in a female Steller sea lion (*Eumetopias jubatus*) pup undergoing

- rehabilitation. *Journal of Zoo and Wildlife Medicine: Official Publication of the American Association of Zoo Veterinarians*, 37(1), 75-78. <https://doi.org/10.1638/04-108.1>
- Pifarré, M., Valdez, R., González-Rebeles, C., Vázquez, C., Romano, M., & Galindo, F. (2012). The effect of zoo visitors on the behaviour and faecal cortisol of the Mexican wolf (*Canis lupus baileyi*). *Applied Animal Behaviour Science*, 136(1), 57-62. <https://doi.org/10.1016/j.applanim.2011.11.015>
- Pritchard, J. C., Lindberg, A. C., Main, D. C. J., & Whay, H. R. (2005). Assessment of the welfare of working horses, mules and donkeys, using health and behaviour parameters. *Preventive Veterinary Medicine*, 69(3-4), 265-283. <https://doi.org/10.1016/j.prevetmed.2005.02.002>
- Reefmann, N., Bütikofer Kaszás, F., Wechsler, B., & Gygax, L. (2009). Physiological expression of emotional reactions in sheep. *Physiology and Behavior*, 98(1-2), 235-241. <https://doi.org/10.1016/j.physbeh.2009.05.017>
- Reif, J. S., Fair, P. A., Adams, J., Joseph, B., Kilpatrick, D. S., Sanchez, R., . . . Bossart, G. D. (2008). Evaluation and comparison of the health status of Atlantic bottlenose dolphins from the Indian River Lagoon, Florida, and Charleston, South Carolina. *Journal of the American Veterinary Medical Association*, 233(2), 299-307. <https://doi.org/10.2460/javma.233.2.299>
- Reiss, D. (2006). Enriching animals while enriching science: Providing choice and control to dolphins. In *Proceedings of the Seventh International Conference on Environmental Enrichment* (pp. 26-31), New York.
- Rietmann, T. R., Stuart, A. E. A., Bernasconi, P., Stauffacher, M., Auer, J. A., & Weishaupt, M. A. (2004). Assessment of mental stress in warmblood horses: Heart rate variability in comparison to heart rate and selected behavioural parameters. *Applied Animal Behaviour Science*, 88(1-2), 121-136. <https://doi.org/10.1016/j.applanim.2004.02.016>
- Riviere, J. E., Engelhardt, F. R., & Solomon, J. (1977). The relationship of thyroxine and cortisol to the moult of the harbor seal *Phoca vitulina*. *General and Comparative Endocrinology*, 31(4), 398-401. [https://doi.org/10.1016/0016-6480\(77\)90027-2](https://doi.org/10.1016/0016-6480(77)90027-2)
- Roe, E., Buller, H., & Bull, J. (2011). The performance of farm animal assessment. *Animal Welfare*, 20(1), 69-78.
- Roelofs, S., Boleij, H., Nordquist, R., & van der Staay, F. J. (2016). Making decisions under ambiguity: Judgment bias tasks for assessing emotional state in animals. *Frontiers in Behavioral Neuroscience*, 10(119), 1-16. <https://doi.org/10.3389/fnbeh.2016.00119>
- Rogers, L. J. (2002). Lateralization in vertebrates: Its early evolution, general pattern, and development. *Advances in the Study of Behavior*, 31, 107-161. [https://doi.org/10.1016/S0065-3454\(02\)80007-9](https://doi.org/10.1016/S0065-3454(02)80007-9)
- Rogers, L. J. (2010). Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science*, 127(1-2), 1-11. <https://doi.org/10.1016/j.applanim.2010.06.008>
- Rushen, J. (2003). Changing concepts of farm animal welfare: Bridging the gap between applied and basic research. *Applied Animal Behaviour Science*, 81(3), 199-214. [https://doi.org/10.1016/s0168-1591\(02\)00281-2](https://doi.org/10.1016/s0168-1591(02)00281-2)
- Russell, J. A. (2003). Core affect and the psychological construction of emotion. *Psychological Review*, 110(1), 145-172. <https://doi.org/10.1037/0033-295X.110.1.145>
- Sakai, M., Morisaka, T., Kogi, K., Hishii, T., & Kohshima, S. (2010). Fine-scale analysis of synchronous breathing in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Behavioural Processes*, 83(1), 48-53. <https://doi.org/10.1016/j.beproc.2009.10.001>
- Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science (New York)*, 308(5722), 648-652. <https://doi.org/10.1126/science.1106477>
- Schwacke, L. H., Smith, C. R., Townsend, F. I., Wells, R. S., Hart, L. B., Balmer, B. C., . . . Rowles, T. K. (2014). Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the Deepwater Horizon oil spill. *Environmental Science and Technology*, 48(1), 93-103. <https://doi.org/10.1021/es403610f>
- Scott, E. M., Mann, J., Watson-Capps, J. J., Sargeant, B. L., & Connor, R. C. (2005). Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour*, 142, 21-44. <https://doi.org/10.1163/1568539053627712>
- Serres, A., & Delfour, F. (2017). Environmental changes and anthropogenic factors modulate social play in captive bottlenose dolphins (*Tursiops truncatus*). *Zoo Biology*, 36(2), 99-111. <https://doi.org/10.1002/zoo.21355>
- Seuront, L., & Cribb, N. (2017). Fractal analysis provides new insights into the complexity of marine mammal behavior: A review, two methods, their application to diving and surfacing patterns, and their relevance to marine mammal welfare assessment. *Marine Mammal Science*, 1-33. <https://doi.org/10.1111/mms.12399>
- Shane, S. H., Wells, R. S., & Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: A review. *Marine Mammal Science*, 2(1), 34-63. <https://doi.org/10.1111/j.1748-7692.1986.tb00026.x>
- Shepherdson, D., Lewis, K. D., Carlstead, K., Bauman, J., & Perrin, N. (2013). Individual and environmental factors associated with stereotypic behavior and fecal glucocorticoid metabolite levels in zoo housed polar bears. *Applied Animal Behaviour Science*, 147(3-4), 268-277. <https://doi.org/10.1016/j.applanim.2013.01.001>
- Shively, C. A., Laber-Laird, K., & Anton, R. F. (1997). Behavior and physiology of social stress and depression in female cynomolgus monkeys. *Biological Psychiatry*, 41(8), 871-882. [https://doi.org/10.1016/S0006-3223\(96\)00185-0](https://doi.org/10.1016/S0006-3223(96)00185-0)
- Small, R. J., & Demaster, D. P. (1995). Survival of five species of captive marine mammals. *Marine Mammal Science*, 11(2), 209-226. <https://doi.org/10.1111/j.1748-7692.1995.tb00519.x>
- Smith, B. P., & Litchfield, C. A. (2010). An empirical case study examining effectiveness of environmental enrichment in two captive Australian sea lions (*Neophoca cinerea*). *Journal of Applied Animal Welfare Science*, 13(2), 103-122. <https://doi.org/10.1080/10888700903371863>

- Sneddon, L. U., Elwood, R. W., Adamo, S. A., & Leach, M. C. (2014). Defining and assessing animal pain. *Animal Behaviour*, 97, 201-212. <https://doi.org/10.1016/j.anbehav.2014.09.007>
- Sobel, N., Supin, A. Ya., & Myslobodsky, M. S. (1994). Rotational swimming tendencies in the dolphin (*Tursiops truncatus*). *Behavioural Brain Research*, 65(1), 41-45. [https://doi.org/10.1016/0166-4328\(94\)90071-X](https://doi.org/10.1016/0166-4328(94)90071-X)
- Spruijt, B. M., van den Bos, R., & Pijlman, F. T. A. (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(2), 145-171. [https://doi.org/10.1016/S0168-1591\(00\)00204-5](https://doi.org/10.1016/S0168-1591(00)00204-5)
- St. Aubin, D. J., & Dierauf, L. A. (2001). Stress and marine mammals. In L. A. Dierauf & F. M. D. Gulland (Eds.), *CRC handbook of marine mammal medicine* (pp. 253-269). Boca Raton, FL: CRC Press. <https://doi.org/10.1201/9781420041637.ch13>
- Stanton, M. A., & Mann, J. (2012). Early social networks predict survival in wild bottlenose dolphins. *PLOS ONE*, 7(10), 1-6. <https://doi.org/10.1371/journal.pone.0047508>
- Tamaki, N., Morisaka, T., & Taki, M. (2006). Does body contact contribute towards repairing relationships? The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. *Behavioural Processes*, 73(2), 209-215. <https://doi.org/10.1016/j.beproc.2006.05.010>
- Tarlow, E. M., & Blumstein, D. T. (2007). Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science*, 102(3-4), 429-451. <https://doi.org/10.1016/j.applanim.2006.05.040>
- Thomson, C. A., & Geraci, J. R. (1986). Cortisol, aldosterone, and leucocytes in the stress response of bottlenose dolphins, *Tursiops truncatus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 43(5), 1010-1016. <https://doi.org/10.1139/f86-125>
- Trone, M., Kuczaj II, S. A., & Solangi, M. (2005). Does participation in dolphin-human interaction programs affect bottlenose dolphin behaviour? *Applied Animal Behaviour Science*, 93(3-4), 363-374. <https://doi.org/10.1016/j.applanim.2005.01.003>
- Ugaz, C., Valdez, R. A., Romano, M. C., & Galindo, F. (2013). Behavior and salivary cortisol of captive dolphins (*Tursiops truncatus*) kept in open and closed facilities. *Journal of Veterinary Behavior: Clinical Applications and Research*, 8(4), 285-290. <https://doi.org/10.1016/j.jveb.2012.10.006>
- Van Bressem, M-F., Van Waerebeek, K., Flach, L., Reyes, J. C., de Oliveira Santos, M. C., Siciliano, S., . . . Castro, C. (2008). Skin diseases in cetaceans. *Reports of the International Whaling Commission* (SC/60/DW8[1975]), 1-11.
- van den Berg, C. L., Pijlman, F. T. A., Koning, H. A. M., Diergaarde, L., van Ree, J. M., & Spruijt, B. M. (1999). Isolation changes the incentive value of sucrose and social behaviour in juvenile and adult rats. *Behavioural Brain Research*, 106(1-2), 133-142. [https://doi.org/10.1016/S0166-4328\(99\)00099-6](https://doi.org/10.1016/S0166-4328(99)00099-6)
- van der Harst, J. E., & Spruijt, B. M. (2007). Tools to measure and improve animal welfare: Reward-related behaviour. *Animal Welfare*, 16(Supp.), 67-73.
- van der Harst, J. E., Baars, A. M., & Spruijt, B. M. (2003). Standard housed rats are more sensitive to rewards than enriched housed rats as reflected by their anticipatory behaviour. *Behavioural Brain Research*, 142(1-2), 151-156. [https://doi.org/10.1016/S0166-4328\(02\)00403-5](https://doi.org/10.1016/S0166-4328(02)00403-5)
- Veissier, I., Butterworth, A., Bock, B., & Roe, E. (2008). European approaches to ensure good animal welfare. *Applied Animal Behaviour Science*, 113(4), 279-297. <https://doi.org/10.1016/j.applanim.2008.01.008>
- Veissier, I., Winckler, C., Velarde, A., Butterworth, A., Dalmau, A., & Keeling, L. (2013). Development of welfare measures and protocols for the collection of data on farms or at slaughter. In H. Blokhuis, M. Miele, I. Veissier, & B. Jones (Eds.), *Improving farm animal welfare: Science and society working together: The Welfare Quality approach* (pp. 115-146). Wageningen, The Netherlands: Wageningen Academic Publishers. [https://doi.org/10.3920/978-90-8686-770-7\\_6](https://doi.org/10.3920/978-90-8686-770-7_6)
- Velarde, A., & Dalmau, A. (2012). Animal welfare assessment at slaughter in Europe: Moving from inputs to outputs. *Meat Science*, 92(3), 244-251. <https://doi.org/10.1016/j.meatsci.2012.04.009>
- Ventre, J., & Jett, J. (2015). Killer whales, theme parks and controversy: An exploration of the evidence. In K. Markwell (Ed.), *Animals and tourism: Understanding diverse relationships* (pp. 1-26). Bristol: UK Channel View Productions.
- Vicino, G. A., & Marcacci, E. S. (2015). Intensity of play behavior as a potential measure of welfare: A novel method for quantifying the integrated intensity of behavior in African elephants. *Zoo Biology*, 34(5), 492-496. <https://doi.org/10.1002/zoo.21238>
- Walker, M. D., Duggan, G., Roulston, N., Van Slack, A., & Mason, G. (2012). Negative affective states and their effects on morbidity, mortality and longevity. *Animal Welfare*, 21, 497-509. <https://doi.org/10.7120/09627286.21.4.497>
- Waples, K. A., & Gales, N. J. (2002). Evaluating and minimizing social stress in the care of captive bottlenose dolphins (*Tursiops aduncus*). *Zoo Biology*, 21(1), 5-26. <https://doi.org/10.1002/zoo.10004>
- Wassel, K., McMann, N., Phillips, C., Demark, C., & Kopf, D. (1996). Enriching seals – Those other marine mammals. *The Shape of Enrichment*, 5, 7-9.
- Watters, J. V. (2014). Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. *Zoo Biology*, 33(4), 251-256. <https://doi.org/10.1002/zoo.21144>
- Webster, J. (2005). *Animal welfare: Limping towards Eden* (UFAW Animal Welfare Series). Oxford, UK: Blackwell Publishing Ltd. [https://doi.org/10.1002/9780470751107\\_fmatter](https://doi.org/10.1002/9780470751107_fmatter)
- Welfare Quality®. (2009a). *Welfare Quality® assessment protocol for cattle*. Lelystad, The Netherlands: Welfare Quality® Consortium.

- Welfare Quality®. (2009b). *Welfare Quality® assessment protocol for pigs*. Lelystad, The Netherlands: Welfare Quality® Consortium.
- Welfare Quality®. (2009c). *Welfare Quality® assessment protocol for poultry*. Lelystad, The Netherlands: Welfare Quality® Consortium.
- Wells, R. S. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies, discoveries and puzzles* (pp. 199-226). Berkeley: University of California Press.
- Wells, R. S. (2009). Learning from nature: Bottlenose dolphin care and husbandry. *Zoo Biology*, 28(6), 635-651. <https://doi.org/10.1002/zoo.20252>
- Whay, H. R., Main, D. C. J., Green, L. E., & Webster, A. J. F. (2003). Animal-based measures for the assessment of welfare state of dairy cattle, pigs and laying hens: Consensus of expert opinion. *Animal Welfare*, 12(2), 205-217.
- Whitham, J. C., & Wielebnowski, N. (2009). Animal-based welfare monitoring: Using keeper ratings as an assessment tool. *Zoo Biology*, 28(6), 545-560. <https://doi.org/10.1002/zoo.20281>
- Whitham, J. C., & Wielebnowski, N. (2013). New directions for zoo animal welfare science. *Applied Animal Behaviour Science*, 147(3-4), 247-260. <https://doi.org/10.1016/j.applanim.2013.02.004>
- Wichman, A., Keeling, L. J., & Forkman, B. (2012). Cognitive bias and anticipatory behaviour of laying hens housed in basic and enriched pens. *Applied Animal Behaviour Science*, 140(1-2), 62-69. <https://doi.org/10.1016/j.applanim.2012.05.006>
- Williams, T. M., Haun, J. E., & Friedl, W. A. (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*) – I. Balancing the demands of exercise for energy conservation at depth. *Journal of Experimental Biology*, 202(20), 2739-2748.
- Yeates, J. W., & Main, D. C. J. (2008). Assessment of positive welfare: A review. *Veterinary Journal*, 175(3), 293-300. <https://doi.org/10.1016/j.tvjl.2007.05.009>