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Managing long-term wellness in captive sea turtles

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Abstract

Circumstances surrounding advances in stranding response and veterinary care have created a growing need for the long-term housing of captive sea turtles. However, the difficulty in recreating natural conditions in captive settings places a responsibility on caregivers to offset wild-type behavioural deficits with enrichment programming that is, preferably, commensurate with the limitations of each enclosure. Though standardised, multi-institutional behavioural monitoring programmes are currently lacking for marine turtles, facilities housing (or planning to house) sea turtles for the long-term are strongly advised to include 'wellness' as a fundamental part of their animal care protocol. Here, concepts of wellness and enrichment in sea turtles are reviewed, and a framework for developing long-term behavioural monitoring programming is provided.

Keywords: *animal welfare, aquarium, behaviour, enrichment, sea turtle, wellness*

Introduction

The growing recognition among both the public and the institutions they support that the physical and emotional well-being, or 'welfare', of long-term captive animals is an important professional and ethical obligation is prompting zoos and aquaria to address these issues among a broad range of taxa (Mellen & Ellis 1996; Barber 2009). Modern exhibit designs are increasingly focused on creating 'naturalistic' surroundings for living collections, and science-based enrichment programmes, many of which are now required for accreditation by the Association of Zoos and Aquariums (AZA), have become the norm at most large institutions (Maple & Lindberg 2008). Broadly defined, animal welfare describes the physical and psychological abilities an animal has to cope with the challenges of its environment (Broom 1988, 1996; Barber & Mellen 2008), and can involve both scientific and ethical questions (Appleby 1997; Sandøe & Simonsen 1992). Webster (2008) simply defined animal welfare as "living a natural life, being fit and healthy, and being happy."

In the realm of animal husbandry, 'environmental enrichment' generally refers to any technique intended to improve the well-being of a captive animal, often through the manipulation of its environment (Newberry 1995). These techniques introduce various stimuli to encourage captive animals to broaden their behavioural spectrum, reinforce desirable behaviours, and/or reduce undesirable ones. Among marine vertebrates, considerable attention has been devoted to the study of cognition and social behaviour of captive marine mammals (Clark 2013), resulting in the development of a suite of environmental enrichment programmes to address their complex needs (Delfour & Beyer 2012). Similarly, enrichment programmes designed for sea turtles have been employed by various aquaria and rehabilitation centres, but few have been described in the literature. Among those, only one quantitatively measured the effects of enrichment on behaviour (Therrian *et al* 2007), but all of them reported 'improvements' in the perceived well-being of the turtles through increased activity levels and reduction of repetitive behaviours (Ethier & Balsamo 2005; Therrien *et al* 2007; Guillen *et al* 2008). Even simple devices such as water jugs, PVC pipes and stationary 'back-scratching' devices elicited exploratory and interactive responses, some evidently species-specific (Guillen *et al* 2008). Though perhaps operating at a slower pace, chelonians are known to have cognitive capabilities such as long-term retention of visual discrimination tasks (Angermeier & Hidalgo 1996; Davis & Burghardt 2012), can learn through social facilitation and stimulus enhancement (Davis 2009), and have spatial and memory capabilities similar to those described in mammals and birds (Lopez *et al* 2000; Wilkinson *et al* 2007). Marine turtles are also equipped with complex optic visual systems that include colour vision (Levenson *et al* 2004; Eckert *et al* 2006), perceive chemical cues via olfaction (Manton *et al* 1972; Grassman & Owens 1982), and recent evidence also suggests that sea turtles perceive sound underwater, particularly in low frequencies (O'Hara & Wilcox 1990; Martin *et al* 2012). As such, permanently captive marine turtles appear to be well-deserving of targeted enrichment programming, but standardised methodologies and monitoring protocols remain absent. More importantly, however, 'wellness' itself in captive marine turtles remains undefined, as do objective measures of the effectiveness of various enrichment options.

As large, wide-ranging marine animals, providing 'natural' surroundings for sea turtles in captivity is difficult or impossible, especially for small- to medium-sized facilities in landlocked locations. As such, captive turtles should not be expected to perform a full suite of natural behaviours or maintain the time budgets observed in their wild counterparts. Additionally, although enrichment plans should optimally be based on what is known of the animal's natural history (Mellen & MacPhee 2001), little is known of sea turtle behaviour in the wild. They can be difficult to locate in the water, and even more difficult to observe for extended periods of time. Researchers have relied upon various remote sensing technologies to infer in-water sea turtle habitat use and behaviour (Hochscheid *et al* 2005; Houghton *et al* 2008; Wilson *et al* 2008; Blumenthal *et al* 2009), and several studies have created ethograms of *in situ* sea turtle activity (van Dam & Diez 1998a; Houghton *et al* 2003; Schofield *et al* 2006; Dunbar *et al* 2008; Blumenthal *et al* 2009; Proietti *et al* 2012; Wood *et al* 2017), but large gaps remain in our understanding of most natural history traits in these species. Nonetheless, enough of a behavioural inventory has been built to begin the discussion of what types of species-appropriate behaviours caretakers should expect to see in captive marine turtles, and how they might be elicited within widely varying institutional constraints.

The exact number of captive sea turtles being held in the US is unknown, though it is currently estimated to be in the hundreds. Some were legally acquired prior to the implementation of the Endangered Species Act 1977 (ESA), but many are survivors of incapacitating injuries and subsequently deemed unable to survive in the wild. In response to a gradually increasing number of sea turtle strandings per year in the South-East US, recovery networks and rehabilitation centres have grown in number and sophistication. The remarkable physical resilience of chelonians combined with today's advanced veterinary treatment options can make choices concerning euthanasia very difficult, leading some turtles back to clinical health, but disabled in some way that precludes their eventual release. These animals then require lifelong care, which may enhance educational and conservation programming, but nonetheless demands a considerable institutional commitment. Chelonians are the longest lived of the reptiles (Castanet 1994), and hard-shelled sea turtles can be expected to live well past 50 years (Zug *et al* 1986). Even the smallest sea turtle species are comparatively large (30+ kg), while the most common species to strand in the SE US (green [*Chelonia mydas*] and loggerhead [*Caretta caretta*]) both exceed 100 kg as adults. They can be aggressive to their aquarium co-habitants, and destructive to their surroundings (LD Wood, personal observation 1992). As larger facilities reach their capacity to take on additional live specimens, increased responsibility will be placed upon smaller organisations to find ways to house these animals for the long-term, where providing sizable enclosures is increasingly limited. Some of these constraints, however, may be sufficiently offset with creative exhibit design and proactive, monitored enrichment programming specifically tailored to the needs of the individual sea turtle(s) under their care.

Defining captive sea turtle wellness

Studies of captive sea turtle behaviour are rare, and a continued lack of wild-type behavioural inventories and time-budgets for sea turtles limits the direct assignment of positive and negative labels to specific behaviours as welfare indicators. Under certain circumstances, behaviours likely considered undesirable in a captive setting (eg stereotypic behaviour or lethargy) may be reflective of an associated life-history trait with its own motivational foundation (eg migratory restlessness or hibernation) (Whitham & Wielebnowski 2013). Nonetheless, among the published reports concerning captive turtle husbandry, there is general agreement on the behaviours that are reflective of either positive or negative psychological well-being. Arena *et al* (2014) evaluated the welfare of farmed sea turtles, and considered panicked hyperactivity, persistent boundary exploration, apprehension, and aggression signs of negative behavioural and psychological arousal. On the other hand, Therrien *et al* (2007) and Guillen *et al* (2008) both considered a reduction in repetitive patterned swimming and increased activity as signs of positive behavioural changes, and Ethier and Balsamo (2005) suggested that increased activity levels reflect positive mental and physical stimulation. Burghardt *et al* (1996) reported marked reductions in self-mutilation behaviour in a captive Nile softshell turtle (*Trionix triunguis*) after engaging the animal with objects such as balls, sticks and hoses. These conclusions are consistent with those presented for captive reptiles as a whole by Warwick *et al* (2013), and with the results of an informal survey of professional captive sea turtle caregivers (Wood unpublished data). Overall, these caregivers associated targeted, curious, and interactive behaviours with positive well-being, and perceived behavioural repetition/stereotyping, excessive lethargy, aggression, and appetite loss as indicators of a negative or stressed psychological state. Once defined, the relative frequency of 'positive' to 'negative' behaviours can be used to indicate the relative state of well-being of a turtle through any given time-period and detect changes if and when they occur. The resulting ratio, or 'wellness score' (*W*) provides caregivers with an objective measure of the psychological state of the turtles under their care, and concrete benchmarks from which behavioural changes can be detected and shared across institutions. Currently, marine reptiles do not automatically receive the institutional commitment to wellness afforded farm animals, primates, or marine mammals, nor has direct oversight thereof been established by any regulatory agencies. Clegg *et al* (2015) based a similar wellness scoring system known as 'C-well' for captive bottlenose dolphins (*Tursiops truncatus*) on the Farm Animal Welfare Quality® Assessment (Welfare Quality® Consortium 2009). Like the scoring system presented here, it enables caregivers to derive a numerical measure of wellness for

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Table 1 Conceptual framework for inferring sea turtle behavioural states. The ratio of the frequency and/or duration of behaviours representative of 'positive' to 'negative' behavioural states is used to assign a wellness score (*W*). This framework can be customised to create ethograms tailored to each subject's life-history and potential physical and/or cognitive limitations.

Behaviour	Definition	Behavioural state
Inactivity	Turtle is immobile; either alert (resting) or comatose (sleeping)	Positive (nocturnal and intermittent diurnal)/negative (excessive; aroused by breathing and external stimuli only)
Exploratory	Attentive, non-repetitive movement; interacting with surroundings but not continuously focused on a single object	Positive
Repetitive	Continuous, patterned repetition of a random, non-targeted behaviour	Negative
Focused	Attentive interaction with an object for at least 5–10 s	Positive
Aggressive	Biting, attacking not related to feeding	Positive (infrequent, non-injurious display)/negative (persistent injurious aggression)
Apprehensive	Active or panicked avoidance	Negative

individual subjects but is intentionally tailored to highly social and intelligent taxa whose overall psychological needs far exceed those of sea turtles; re- C-well incorporates thirty-six separate measures representing eleven criteria. Later, Justice *et al* (2017) presented a computer-based adaptation of the animal welfare assessment grid (AWAG) (Honess & Wolfensohn 2010), which calculates a Cumulative Welfare Assessment Score (CWAS) based on a combination of physical, behavioural/psychological, environmental, and procedural parameters. Though reputedly applicable to any species, AWAG was specifically designed for non-human primates, and has not yet been proven in non-mammalian species (Ryan *et al* 2021). Here, the framework for a simple, easy-to-use, in-house systematic scoring system is provided that can be readily adapted to a level commensurate with the limitations and/or desires of individual sea turtle caregivers, including those who may not have received formal animal husbandry training.

Measuring sea turtle wellness

In human psychology, the concept of 'positivity' suggests that people with higher ratios of positive to negative emotions tend to have more satisfying and productive lives (Frederickson & Losada 2005). Though the mathematical underpinnings of their specific conclusions have been questioned (Brown *et al* 2013), most of us would intuitively agree that a high positivity/negativity ratio is reflective of a more pleasant life experience than a low one, leading to an increased state of well-being that may not be unique to humans. Without the benefit of verbal communication, assessments of animal 'emotion' becomes solely restricted to behavioural interpretation. Therefore, we can look to the suite of behaviours commonly exhibited by sea turtles in captivity as at least partial expressions of their overall well-being and seek to maintain high ratios of 'positivity' among captive specimens.

Given subtle differences across taxa and individual sea turtles, there is a general consensus that two easily recognisable behaviours surface as signs of negative or stressful states: (i) repetitive/stereotyped behaviour; and (ii) panicked apprehension. Likewise, two other behaviours: (i) exploratory; and (ii) focused are considered reflective of positive mental states. Inactivity and aggression are also common behaviours that could be considered, based on their relative frequencies. These behaviours are defined and summarised in Table 1.

Though reliable time budgets for wild sea turtles remain difficult to describe (Fuller *et al* 2009), most hard-shelled sea turtles are believed to be largely inactive at night (Ogden *et al* 1983; van Dam & Diez 1997; LD Wood personal observation 2004), and periods of day-time resting are common (Schofield *et al* 2006). In the wild, energy management and balance ultimately determine time budgets (Hochscheid *et al* 2005), and though day-time resting conserves energy and may also function as an anti-predator behaviour, sufficient time must also be allotted to foraging. Without this pressure, captive turtles are likely to develop different time budgets than their wild counterparts that may include a shift toward increased lethargy. Among the few studies that have attempted to create *in situ* behavioural inventories, wild loggerheads were observed resting between 20 and 60% of the time during the day (Schofield *et al* 2006), and hawksbill (*Eretmochelys imbricata*) observations reported resting in between 20.3 ($n = 50$) and 33% ($n = 317$) of the individuals observed (Blumenthal *et al* 2009; Proetti *et al* 2012). In a captive setting, Therrien *et al* (2007) recorded a decrease in resting frequency from 38% without enrichment to 5% in the presence of enrichment stimuli. Clearly, quiescence reflects general contentment, and is a normal part of a sea turtle's daily behavioural regimen, but excessive lethargy (in excess of 75% of the daily activity budget) may also represent behavioural inhibition, which can be a sign of chronic stress (Warwick *et al* 2013).

In the wild, sea turtles are believed to be largely solitary animals (Hays *et al* 2002; Murphy-Hopkins *et al* 2003; Blumenthal *et al* 2009); but are also known to form periodic mating and foraging site aggregations that often contain

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Table 2 Conceptual framework for numerically appraising the inanimate/immobile features, ie 'static stimuli (S_s)' of a sea turtle enclosure.

Feature	Definition	Point value
Partial cover	Vertical surface under which a turtle can place its head and/or up to 50% of its carapace	1 each
Full cover	Vertical surface under which a turtle can place its head and/or up to 100% of its carapace	1 each
Patterns	Stationary black and white or single colour patterns	1
Colour	Stationary multi-coloured objects or patterns	1
Complex shapes	Multi-dimensional objects; swim-throughs	1 each
Resting surfaces	Off-bottom platform; multiple resting depths	1

Table 3 Conceptual framework for numerically appraising animated/mobile stimuli, ie 'active stimuli (S_a)' in and around a sea turtle enclosure.

Feature	Definition	Point value
Natural light cycle	Outdoor/semi-outdoor/ cycled artificial lighting	1
Live animals (single taxa)	1 or more of the same species of mobile/animated organisms (fish, invertebrates)	1
Live animals (multiple taxa)	2 or more species of mobile/ animated organisms (fish, invertebrates)	1
Other turtles	1 or more additional sea turtles	1
Moveable objects	Non-stationary, non-living objects that can be moved or manipulated by a turtle	1 each
Extra-enclosure stimuli	Visual/audial stimuli originating from outside the enclosure: weather; human activity; floral/faunal activity	1 each

Table 4 Conceptual framework for scoring directed enrichment provided to the turtle, ie 'directed stimuli (S_d)' by enrichment category. Directed stimuli can be very effective in offsetting potential deficiencies in other forms of environmental stimuli and can have profound effects on behavioural modification.

Enrichment	Definition	Score (per event)
Problem solving	Task accomplished through specific behaviours, eg food 'puzzles'	1
Persistence	Task accomplished through persistence, eg frozen food blocks	1
Association	Task accomplished through training, eg target training	1
Tactile	Physical contact, eg scrubbing/rubbing/ cleaning/sparring	1

overlapping individual home ranges. When not engaged in reproductively motivated competitive combat, aggression among sea turtles is largely the result of mild territoriality among conspecifics at both foraging and resting sites. These disputes are typically resolved with eye contact and open-mouthed, head-to-tail circling, most often resulting in the departure of the more submissive individual without physical contact (Schofield *et al* 2006; LD Wood, personal observation 2012). In captivity, however, options for peaceful resolutions decrease with space limitations and overcrowding. Aggressive behaviour between green turtles was classified as 'frequent' and 'common' in Arena *et al*'s (2014) assessment of the exceptionally crowded conditions they observed at Cayman turtle farm, while more reasonably scaled housing for multiple turtles has proven quite successful in a number of other captive settings (LD Wood, personal observation 2000).

In the framework presented here, the caretaker actively influences the subject's behavioural repertoire through simple environmental manipulation, with the expressed goal of maintaining or increasing the ratio of positive to negative behaviours (W) (Table 1). The most basic features of a sea turtle enclosure consist of its capacity (C), including total volume (v), and maximum depth (d), the presence of non-moving objects (static stimuli; S_s) (Table 2), and the presence of mobile/animated objects (active stimuli; S_a) (Table 3). Combined, they comprise the daily experience of the turtle of a given size without the direct intervention of a caregiver. In addition to the stimuli associated with the features of the enclosure, human-directed activities (feeding/tank cleaning/interacting, etc) provide additional periodic stimuli (S_d) (Table 4). Conceptually:

$$W \propto C_{(v/SCL\ +\ d/SCL)} + S_s + S_a + S_d$$

where the wellness score (W) is proportional to the sum of the enclosure's capacity (volume [v] and maximum depth [d]) per size turtle (SCL) and a combined numerical assessment of the environmental stimuli ($S_s + S_a$) and directed stimuli (S_d) the turtle experiences over time. This framework permits a caregiver to evaluate each of these variables independently, and through experimental manipulation, determine how each may be influencing a turtle's overall wellness score (W). For example, the larger and deeper the enclosure, the presumably 'better' for a sea turtle, but without additional stimuli of some kind, repetitive and stereotyped behaviours are likely to persist. Alternatively, comparatively small enclosures may restrict freedom of movement to varying degrees, but supplemental environmental and/or directed stimuli may offset the negative psychological effects of varying levels of confinement. To best care for these animals in the long term, institutions have an obligation to objectively measure and maintain wellness in their captive turtles, and adaptively balance the above parameters in a way that achieves and maintains high wellness scores.

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Enclosure capacity (*C*)

Given the natural history of sea turtles, all man-made enclosures will restrict their behavioural inventory to some degree. The considerable expense of constructing and maintaining saltwater aquaria has limited the number of facilities that can even remotely provide 'naturalistic' conditions (100,000+ gallons [378,540+ L]) for adult turtles, placing a larger responsibility on smaller facilities to accommodate a growing number of non-releasable specimens. Though no peer-reviewed studies have directly related enclosure size to the behaviour of captive sea turtles, it stands to reason that increased levels of confinement will lead to increased levels of stress. This does not necessarily mean, however, that moderately sized enclosures cannot be designed to provide sufficient balance of space and stimuli to maintain physically and psychologically healthy sea turtles on a long-term basis.

The Florida Fish and Wildlife Conservation Conservation (FWC) and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST) have jointly published USFWS-based guidelines for holding-tank capacities based on turtle size class as measured by straight carapace (shell) length (SCL) and width (SCW) (Bluvias & Eckert 2010; United States Department of the Interior Fish and Wildlife Service [USFWS] 2013). In summary, small turtles (< 10 cm) must be given an enclosure with a surface area of at least five times their length, medium turtles (divided into two classes: < 50 cm and < 65 cm) at least seven times their length, and large turtles (> 65 cm) at least nine times their length, by at least twice each's width at all stages. For reference, on average, most hard-shelled sea turtle species are approximately 20% longer than they are wide throughout their lives (Caldwell 1962; van Dam & Diez 1998b). Minimum depth requirements increase incrementally for each size class from one foot (30.5 cm) to 2.5 feet (76.2 cm) to three feet (91.4 cm) to four feet (121.9 cm), respectively. For reference, using these guidelines, the minimum volume for a 65-cm turtle would be approximately 1,140 gallons (4,325 L), and a 90-cm turtle approximately 3,760 gallons (14,230 L). The guidelines also require an incremental increase in surface area by 25, 50, and 100% per size class, respectively, for each additional turtle added per enclosure. Though these recommendations provide minimum space guidelines for all captive sea turtles, regardless of their expected time in captivity, they were developed primarily for relatively short-term housing scenarios, eg while under veterinary/recuperative care, and therefore should be considered grossly inadequate for the optimal long-term care of unreleasable specimens.

Given these guidelines, it is possible to objectively evaluate an enclosure based on the ratio of its capacity to the size of the turtle(s) within. Under most circumstances, sea turtle enclosures (often round or irregularly shaped liquid holding tanks), are designed and measured by volume and depth, rather than surface area. This being the case, a simple calculation provides an enclosure-volume-to-turtle-size ratio (L/SCL [cm]), and depth ratio (max depth/SCL [cm]) for each specimen. The minimum recommended 'capacity scores' for both volume and depth can be determined per size class for solitary turtles. When necessary, minimum capacity scores for multiple turtles can be calculated by using the sum of the straight carapace lengths of each tank co-habitant.

Static (S_s) and active (S_a) stimuli

Enclosure size is only one component of the turtle's experience that may influence the continued development and maintenance of positive behavioural states. In the wild, sea turtles are immersed in a wide variety of structurally, texturally, and biologically complex and colourful environments which cannot be reproduced to their full extent in captive settings. There are, however, particular features of these environments that are known to elicit predictable responses in sea turtles. Among the most important of these is quiescence associated with protective refuge (Proetti *et al* 2012). In the wild, underwater structures create low-light, multidimensional micro-habitats that provide protection from currents and predators, and potentially extend submergence times by counteracting mild positive buoyancy at depth, aka 'assisted resting' (Houghton *et al* 2003).

Additionally, overhead structures provide surfaces for tactile stimulation, particularly the 'rubbing' of the carapace, which likely serves as a form of grooming behaviour (Frick & McFall 2007). Wild and captive turtles, particularly green turtles, are known to vigorously rub their carapaces on textured overhead surfaces with rapid body rotations (Frick & McFall 2007; Guillen *et al* 2008; LD Wood, personal observation 1990).

In order to evaluate an enclosure's capacity to provide static and active stimuli to the turtle(s) residing within, a customised, in-house scoring system can be employed that assigns the enclosure two simple numerical 'scores' for use in the wellness equation. Given the known behavioural repertoire of sea turtles, a featureless tank of water, no matter the volume, provides intuitively less stimuli than one containing structures, objects, and/or opportunities to interact with other organisms. Within the framework of this system, points can be assigned for each form of active and static stimuli the turtles are exposed to, and when summed, allows caregivers to objectively appraise the quality of the enclosure in question (Tables 2 and 3). Since all facilities are different, potential deficiencies in one form of stimuli can be compensated for by others. Conceptually, as static and active stimuli are added and/or removed, some commensurate behavioural response from the turtle(s) should be expected, at least in the short-term. For example, an empty tank of water would accrue very low S_s and S_a scores. As stimuli are introduced (ie numerically increasing S_s and/or S_a) and new behaviours are recorded, each turtle's wellness score will begin to fluctuate. Given the stated goal of improving each subject's wellness score, caregivers can evaluate the effectiveness of adding and/or removing each form of stimuli alone or in combination, and continuously 'tweak' the system to boost and maintain high wellness scores over time.

Directed stimuli (S_d)

Directed stimuli consist of human-controlled activities or stimuli that are not encountered in the animal's regular daily environment. This factor in the wellness equation allows for the most creativity and flexibility on the part of the caregiver; and is crucial to offsetting the various limitations of the enclosures and their features themselves. Routine animal care, such as feeding, cleaning, and periodic medical examination, are all forms of directed stimuli. Additionally, there may be other activities in the enclosure that are not directed at the turtles themselves but provide additional periodic stimulation of some kind (eg feeding/caring for other enclosure inhabitants; enclosure maintenance; diving encounters, etc).

There are four basic categories of directed enrichment for sea turtles in use today: activities that involve association (aka 'training'), problem-solving, persistence, and tactile stimulation (Table 4). The most controlled form of directed stimulation involves targeted behavioural enrichment, where specific behaviours are elicited by introducing specific, pre-designed stimuli. Given the motivation to do so, sea turtles will actively engage with their surroundings and caregivers and can be trained to perform a number of desired behaviours (Ethier & Balsamo 2005). In some cases, caregivers have found training crucial for increasing the ease with which very large individuals can be controlled and manipulated, and reducing the stress associated with competition for food and routine maintenance/health assessments.

Studies have probed the neuroscience that underlies the ability of reptiles to learn (eg Holtzman *et al* 1999; Almli & Burghardt 2006; Emer *et al* 2015), and they are known to respond to operant conditioning (Hellmuth *et al* 2012). It is also understood that environmental enrichment has wide-ranging effects on the brain at multiple levels, and that neural plasticity increases with learning (Kotloski & Sutula 2015). Therefore, activities that encourage the turtle to make appropriate choices while seeking a reward are not outside the turtles' capabilities, and may in fact have positive long-term health benefits. 'Puzzles' that require some specific action or series of actions on the turtles' part to receive a reward can include food containers that require some sort of manipulation to open, or the positioning of a desired object in such a way that requires a particular series of manoeuvres to obtain. For carnivorous species, the introduction of live food items that require some specific handling prior to consumption (eg crustaceans, molluscs) may also be considered, but administered appropriately given concerns about parasite introduction and/or injury to the turtle.

Alternatively, enrichment techniques that encourage persistence are also highly effective, and widely used among sea turtle caregivers (LD Wood, personal observation 2015). These techniques do not require the turtle to perform any specific task(s) prior to receiving the reward, rather they increase the challenges associated with obtaining the reward itself. For example, food items frozen into blocks of ice or placed in hard-to-reach places require extended food-handling time that is rewarded only after some period of focused effort.

As briefly mentioned before, wild-type behaviours suggest that some sea turtles seek tactile stimulation through vigorous rubbing of their shells (both carapace and plastron), which is likely associated with epibiont removal (Frick & McFall 2007; LD Wood, personal observation 2005). Aside from self-grooming, hard-shelled sea turtles are also known to repeatedly visit 'cleaning stations' at or near coral reefs where multiple species of fish (eg wrasses, tangs, angelfish, etc) leave the reef to pick epibiota from their skin and shell (see Sazima *et al* 2010). The desire among some individuals to make physical contact with objects is commonly reported among caregivers, both in the form of shell-scrubbing and biting/sparring with cleaning tools (Therrien *et al* 2007; Guillen *et al* 2008; LD Wood, personal observation 1995).

As with the active (S_a) and static (S_s) sources of stimuli, the various forms of directed stimuli (S_d) provided to the turtle can be scored within the framework of the wellness equation. Clearly, however, what might work for one turtle may not for another, and varying preferences for and responses to directed stimuli have been documented among individuals and species in captive settings (Burghart *et al* 1996; Ethier & Balsamo 2005; Guillen *et al* 2008). Knowing the individual physical limitations or preferences of the turtles themselves, caregivers can tailor enrichment programming for each subject under their care to achieve the desired outcomes.

Monitoring sea turtle wellness

The efficacy of enrichment methodologies can only be assessed by their individual or collective influence on the subject's behaviour over time. Without good data in hand, however, an objective baseline measure of wellness cannot be established, nor can behavioural changes be evaluated. Behavioural monitoring programmes (BMPs) can generate these data and provide caregivers with an objective and consistent inventory of what an animal has been doing, thus providing the basic information required to measure wellness in the long-term. These programmes only work, however, when all participants agree on the definitions of the specific behaviours being observed and commit to a pre-determined data collection protocol (Watters *et al* 2009). In the case of sea turtles, behavioural inventories do not need to be extensive, nor does behavioural monitoring necessarily require considerable time or effort. Still, however, having some way to measure and evaluate behaviour is at the core of any casual or hypothesis-driven inquiry into captive turtle wellness.

The first step in developing a BMP is to create an ethogram, or list of behaviours that the subject is known to perform. The ethogram need not include an extensive suite of behavioural subtleties but should at least include those behaviours that comprise most of the subject's time budget, and/or those that are clearly reflective of either positive or negative mental states (Watters *et al* 2009). No matter what they are, it is imperative that the behaviours included in the ethogram are clearly defined at the outset, and all observer participants interpret them consistently. The six behaviours listed in Table 1 can be used as the basis for a comprehensive captive sea turtle ethogram.

The next step is determining the basic regime under which the data are collected.

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Observations can be 'continuous', where behavioural transitions are recorded through a pre-determined period of time (eg recording the duration of everything the turtle did for 15 consecutive minutes), or 'instantaneous', where data are recorded at specific points or intervals of time (eg the specific action the turtle was performing at each of three 5-min intervals within a 15-min span). Both regimes allow for considerable flexibility, especially when faced with the realities of caregiver time management. In fact, neither necessarily require particularly large blocks of time. Several continuous observations for as little as 10 min at a time, or as few as 8–10 randomly spaced instantaneous observations per day can begin to create reasonable time-budget estimates (Margulis & Westhus 2007; Watters *et al* 2009). Even an ethogram that defines behaviour in no more detail than as simply 'active' or 'inactive' lays the foundation for monitoring basic activity levels as the data accumulate over time.

It is also important that each behavioural observation, however simple it may be, is placed in some sort of relevant context. In the example of a point observation that only includes 'active' or 'inactive' states, at least one measurable, non-fixed covariate must be chosen to which those behavioural states are associated, for example, the time of day. In more detailed ethograms, covariates can be ranked by their likely relationship to the behaviours most frequently observed or chosen for their experimental value. For example, if aggression was observed between turtles, was there a likely cause such as competition for food or space? If focused behaviour was observed, what was the object of the focus? Within the framework of the wellness ratio (*W*) introduced here, the various forms of stimuli defined in Tables 2–4 create a comprehensive list of covariates that can be experimentally manipulated to determine their influence on the frequency of certain behaviours. For example, simply adding a colour pattern to the sides of a featureless enclosure may reduce stereotyped behaviour or introducing live companions (of any kind) may increase activity levels. Either way, it will be up to the caregivers themselves to adopt a BMP commensurate with the wellness goals of their respective institutions.

Aside from observer training, data management and interpretation can be the most time-consuming aspects of any behavioural monitoring programme (Watters *et al* 2009). Mental notes and paper-and-pencil observations are very useful but gain considerable value when they coalesce into a dataset that can be organised, interpreted, and shared. At its core, the wellness score (*W*) is simply an unbiased ratio of the frequencies of two basic, agreed-upon classes of behaviours, ie the 'good' ones versus the 'bad' ones. However, based on the BMP standards set by caregivers, both of these broad behavioural classes can be subdivided and examined with increasing complexity. Once the standard of measurement for (*W*) is set, the effects of individually or collectively manipulating the variables on the right side of the equation (C, S_s, S_a, and S_d) can begin to be determined. Though plenty of statistical tests are available for analysing observational data (Kuhar 2006; Therrien *et al* 2007; Watters *et al* 2009), simply charting the wellness ratio (*W*) against the enrichment score calculated for each turtle's environment provides enough feedback to establish a baseline from which changes can be detected through time, and a format that can be shared among institutions. For more advanced analyses, a number of professional-grade tools are available for recording and analysing behaviour, such as JWatcher™, The Observer™, BORIS©, and others.

Animal welfare implications

Marine megafauna, by their very nature, present unique challenges regarding animal welfare. Even the most basic husbandry requirements for these animals (eg diet, enclosure, water quality, etc) are both expensive and technically challenging, and these species tend to be highly social, have complex lifecycles, and/or are often fairly long-lived. Comparatively, hard-shelled sea turtles are fairly easy to maintain in the short-term; they are notoriously hardy, adapt well to captive settings, and accept a broad range of food items. These traits allow for a flourishing consortium of sea turtle rehabilitation centres that achieve high rates of success in re-releasing the patients in their care. However, without considerable planning, even well-intended attempts at keeping sea turtles permanently often comes at the cost of the well-being of the animals themselves.

In the vast majority of cases, sea turtles enter captivity under some sort of duress, and due to their conservation status, are often ultimately the responsibility of wildlife authorities. Nonetheless, decisions concerning the animals' prognoses are best made by veterinary professionals, who then either initiate a treatment plan or, by necessity, prescribe euthanasia as a last resort. In all cases, the preferred outcome is the release of the animal back to the wild. Over the years, experts have made remarkable progress in developing and implementing sea turtle rehabilitation techniques (see Manire *et al* 2017), but relatively little attention has been paid to the potential effects of sub-optimal housing conditions on the health and well-being of those under permanent care. Given the lack of standardised protocols to measure wellness in sea turtles, the system presented here provides the conceptual framework for a simple, easy-to-use tool that can easily be adapted for use in a broad range of settings and has the potential to substantially improve the welfare of captive sea turtles.

Conclusion

The slow but steady recovery of sea turtle populations in the Atlantic basin is very likely the outcome of several decades of targeted conservation strategies, and cautious optimism is well-deserved for their short- and medium-term futures. Though some populations still struggle, the SE coast of the US, in particular, has experienced remarkable increases in nesting activity since 2000 (Fl Marine Research Institute unpublished data; Valdivia *et al* 2019). Circumstances surrounding these events have led to a higher relative abundance of turtles in coastal areas, where human interaction (often the root cause of the injury or illness) is most likely. Inevitably, the number of turtles requiring human intervention will continue to rise as further success is realised throughout the region.

In the US, stranding response protocols are in place for most coastal areas where sea turtles are known to occur. Networks of volunteers and rehabilitation facilities work closely with government agencies to respond to turtles in need. Sea turtle rehabilitation centres have kept pace with advances in veterinary care, leading to in-depth treatment plans that can rival human patient care. Then, once the turtles are restored to health, the process often culminates in well-choreographed celebrations surrounding their return to the wild. The situation becomes considerably more complex, however, when the presenting injuries include those that may affect basic survival skills.

Currently, there is no standard, multi-institutional list of conditions that automatically preclude a sea turtle's eventual release to the wild. The final determination whether to either begin treatment on the patient, or subsequently, whether to release a physically handicapped animal is made by the facility's staff, usually advised by an attending veterinarian. Concerns for quality of life guide the difficult decisions that veterinarians must make concerning euthanasia, which can be made even more difficult with the uncertainties associated with treating wild animals. There is general agreement among the sea turtle rehabilitation community, however, that total blindness, multiple amputations, and severe buoyancy abnormalities associated with paralysis are not conducive to long-term survival in the wild (LD Wood, personal observation 1995). While some of these prognoses may be apparent upon initial presentation, many others are not so easily made, and require some period of time before making decisions concerning eventual releasability. Nonetheless, if any of these or other survival-negating outcomes appear inevitable at some point, those that do recover would eventually require intensely supportive life-long care which, in most cases, cannot be provided by the rehabilitation facilities themselves. With suitable 'permanent homes' becoming increasingly difficult to find, rehabilitation facilities will bear increasing responsibility for making informed decisions not only about the short-term medical treatment of these animals, but also the long-term needs of those that end up recovering. The adoption of 'non-release plans' that include pre-determined permanent housing commitments for each incoming patient may be an important step toward addressing impending overcrowding issues.

Given strong institutional commitments to ensuring the health of their collections, turtles that are consigned to permanent captivity should never be simply and indefinitely 'stored away' as a result of avoiding difficult decisions. Physical and psychological well-being should not be a privilege restricted to those turtles fortunate enough to reside in spacious, naturalistic surroundings, nor to only those whose keepers have extensive behavioural monitoring/enrichment experience. The methods presented here provide a universal framework for assessing the surroundings and behaviour of captive sea turtles under all circumstances, and introduces an objective, measurable set of evaluations that hopefully encourages increasingly creative, outcome-oriented behavioural monitoring programmes.

Declaration of interest

None.

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References

Almli L and Burghardt G 2006 Environmental enrichment alters the behavioral profile of ratsnakes (*Elaphe*). *Journal of Applied Animal Welfare Science 9(2)*: 85-109. https://doi.org/10.1207/s15327604jaws0902_1

Angermeier WF and Hidalgo ARS 1996 Food-rewarded operant learning and memory in the East Pacific green turtle. *Marine Turtle Newsletter 75*: 4-6

Appleby MC 1997 Life in a variable world: behavior, welfare and environmental design. *Applied Animal Behaviour Science 54*: 1-19. https://doi.org/10.1016/S0168-1591(96)01197-5

Arena PC, Warwick C and Steedman C 2014 Welfare and environmental implications of farmed sea turtles. *Journal of Agricultural and Environmental Ethics 27(2)*: 309-330. https://doi.org/10.1007/s10806-013-9465-8

Barber JCE 2009 Programmatic approaches to assessing and improving animal welfare in zoos and aquariums. *Zoo Biology 28*: 519-530. https://doi.org/10.1002/zoo.20260

Barber JCE and Mellen J 2008 Assessing animal welfare in zoos and aquariums: is it possible? In: Bettinger T and Bielitzki J (eds) *The Well-being of Animals in Zoo and Aquarium Sponsored Research: Putting Best Practices Forward* pp 39-52. Scientists Center for Animal Welfare: Green Belt, MD, USA

Blumenthal JM, Austin TJ, Bell CDL, Bothwell JB, Broderick AC, Ebanks-Petrie G, Gibb JA, Luke KE, Olynik JR, Orr MF, Solomon JL and Godley BJ 2009 Ecology of hawksbill turtles, *Eretmochelys imbricata*, on a Western Caribbean foraging ground. *Chelonian Conservation and Biology 8*: 1-10. https://doi.org/10.2744/CCB-0758.1

Bluvias JE and Eckert KL 2010 *Marine turtle trauma response procedures: A husbandry manual. Wider Caribbean Sea Turtle Conservation Network (WIDECAST) Technical Report No 10*. pp 1-100. Ballwin: Missouri, USA

Broom DM 1988 The scientific assessment of animal welfare. *Applied Animal Behaviour Science 20*: 5-19. https://doi.org/10.1016/0168-1591(88)90122-0

Broom DM 1996 Animal welfare defined in terms of attempts to cope with the environment. *Acta Agriculturae Scandinavica-A 27*: 22-28

Brown NJ, Sokal AD and Friedman HL 2013 The complex dynamics of wishful thinking: the critical positivity ratio. *American Psychologist 68(9)*: 801-13. https://doi.org/10.1037/a0032850

Burghardt GM, Ward B and Rosscoe R 1996 Problem of reptile play: Environmental enrichment and play behavior in a captive Nile soft-shelled turtle, *Trionyx triunguis*. *Zoo Biology 15*: 223-238. https://doi.org/10.1002/(SICI)1098-2361(1996)15:3

https://doi.org/10.7120/09627286.31.4.007 Published online by Cambridge University Press

Caldwell DK 1962 *Carapace Length: Body Weight Relationship and Size and Sex Ratio of the Northeastern Pacific Green Sea Turtle*, Chelonia Mydas Carrinegra. Los Angeles County Museum: CA, USA

Castanet J 1994 Age estimation and longevity in reptiles. *Gerontology 40*: 174-192. https://doi.org/10.1159/000213586

Clark FE 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/10.19227/jzar.v1i1.19

Clegg ILK, Borger-Turner JL and Eskelinen HC 2015 C-Well: The development of a welfare assessment index for captive bottlenose dolphins (*Tursiops truncatus*). *Animal Welfare 24*: 267-282. https://doi.org/10.7120/09627286.24.3.267

Davis KM 2009 *Sociality, cognition, and social learning in turtles (*Emydidae*)*. PhD Dissertation, University of Tennessee, USA

Davis KM and Burghardt GM 2012 Long-term retention of visual tasks by two species of *Emydid turtles, Pseudemys nelsoni* and *Trachemys scripta*. *Journal of Comparative Psychology 126(3)*: 213-223. https://doi.org/10.1037/a0027827

Delfour F and Beyer H 2012 Assessing the effectiveness of environmental enrichment in bottlenose dolphins (*Tursiops truncatus*). *Zoo Biology 31*: 137-150. https://doi.org/10.1002/zoo.20383

Dunbar SG, Levenson D and Crognale M 2008 In-water observations of recently released juvenile hawksbills (*Ertetmochelys imbricata*). *Marine Turtle Newsletter 121*: 5-9

Eckert S, Levenson D and Crognale M 2006 *The sensory biology of sea turtles: what can they see, and how can this help them avoid fishing gear. Sea turtle and pelagic fish sensory biology: developing techniques to reduce sea turtle bycatch in longline fisheries* p 8e16. NOAA Technical Memorandum NMFS-PIFSC-7, National Marine Fisheries Service, December 2006. https://www.bmis-bycatch.org/system/files/zotero_attachments/library_1/ZQ7KAHJS%20-%20Swimmer%20and%20Brill%20-%202006%20-%20Sea%20turtle%20and%20pelagic%20fish%20sensory%20biology%20devel.pdf#page=18

Emer SA, Mora CV, Harvey MT and Grace MS 2015 Predators in training: operant conditioning of novel behavior in wild Burmese pythons (*Python molurus bivitattus*). *Animal Cognition 18(1)*: 269-278. https://doi.org/10.1007/s10071-014-0797-1

Ethier N and Balsamo C 2005 Training sea turtles for husbandry and enrichment. *Proceedings of the Seventh International Conference on Environmental Enrichment* pp 106-111. 31 July-5 August 2005, New York, USA

Fredrickson BL and Losada MF 2005 Positive affect and the complex dynamics of human flourishing. *American Psychologist 60(7)*: 678-86. https://doi.org/10.1037/0003-066X.60.7.678

Frick MG and McFall G 2007 Self-grooming by loggerhead sea turtles in Georgia, USA. *Marine Turtle Newsletter 118*: 15

Fuller WJ, Broderick AC, Hooker SK and Witt MJ 2009 Insights into habitat utilization by green turtles (*Chelonia mydas*) during the internesting period using animal borne digital cameras. *Marine Technology Society Journal 43(3)*: 51-59. https://doi.org/10.4031/MTSJ.43.3.4

Grassman MA and Owens DW 1982 Development and extinction of food preferences in the loggerhead sea turtle, *Caretta caretta. Copeia 1982(4)*: 965-969. https://doi.org/10.2307/1444110

Guillen L, Marcum H and George J 2008 Behavioral impact of enrichment tools on captive sea turtles. *Proceedings of the 27th Annual Symposium on Sea Turtle Biology and Conservation: NOAA Technical Memorandum NMFS-SEFSC-569* p 17. 24 February-1 March 2007, Myrtle Beach, South Carolina, USA

Hays GC, Glen F, Broderick AC, Godley BJ and Metcalf JD 2002 Behavioural plasticity in a large marine herbivore: Contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. *Marine Biology 141*: 985-990. https://doi.org/10.1007/s00227-002-0885-7

Hellmuth H, Augustine L, Watkins B and Hope K 2012 Using operant conditioning and desensitization to facilitate veterinary care with captive reptiles. *Veterinary Clinics of North America: Exotic Animal Practice 15*: 425-443. https://doi.org/10.1016/j.cvex.2012.06.003

Hochscheid S, Maffucci F, Bentivegna F and Wilson RP 2005 Gulps sneezes and sniffs: how measurement of beak movement in sea turtles can elucidate their behavior and ecology. *Journal of Experimental Marine Biology and Ecology 316*: 45-53. https://doi.org/10.1016/j.jembe.2004.10.004

Holtzman DA, Harris TW, Aranguran G and Bostock E 1999 Spatial learning of an escape task by young corn snakes, *Elaphe guttata guttata*. *Animal Behaviour 57(1)*: 51-60. https://doi.org/10.1006/anbe.1998.0971

Honess P and Wolfensohn 2010 The extended welfare assessment grid: A matrix for the assesssment welfare and cumulative suffering in experimental animals. *Alternatives to Laboratory Animals 38(3)*: 205-212. https://doi.org/10.1177/026119291003800304

Houghton DR, Callow MJ and Hays GC 2003 Habitat utilization by juvenile hawksbill turtles (*Eretmochelys imbricata*, Linneaus 1776) around a shallow water coral reef. *Journal of Natural History 37(10)*: 1269-1280. https://doi.org/10.1080/00222930110104276

Houghton DR, Cedras A, Myers AE, Liebsch N, Metcalfe JD, Mortimer JA and Hays GC 2008 Measuring the state of consciousness in a free-living diving sea turtle. Journal of *Experimental Marine Biology and Ecology 356*: 115-120. https://doi.org/10.1016/j.jembe.2007.12.008

Justice WSM, O'Brien MF, Szyska O, Shotton J, Gilmour JEM, Riordan P and Wolfenson S 2017 Adaptation of the animal welfare assessment grid (AWAG) for monitoring animal welfare in zoological collections. *Veterinary Record 181(6)*: 143. https://doi.org/10.1136/vr.104309

Kotloski RJ and Sutula TP 2015 Environmental enrichment: Evidence for an unexpected therapeutic influence. *Experimental Neurology 264*: 121-126. https://doi.org/10.1016/j.expneurol.2014.11.012

Kuhar CW 2006 In the deep end: Pooling data and other statistical challenges of zoo and aquarium research. *Zoo Biology 25*: 339-352. https://doi.org/10.1002/zoo.20089

Levenson DH, Eckert SA, Crognale MA, Deegan JFI and Jacobs GH 2004 Photopic spectral sensitivity of green and loggerhead sea turtles. *Copeia 4*: 908-914. https://doi.org/10.1643/CP-03-217R1

Lopez JC, Rodriguez F, Gomez Y, Vargas JP, Broglio C and Salas C 2000 Place and cue learning in turtles. *Animal Learning and Behavior 28(4)*: 360-272. https://doi.org/10.3758/BF03200270

Manire CA, Norton TM, Stacy BA, Innis CJ and Harms CA 2017 *Sea Turtle Health & Rehabilitation*. J Ross Publishing: Plantation, Florida, USA

Manton M, Karr A and Ehrenfeld DW 1972 Chemoreception in the migratory sea turtle, *Chelonia mydas*. *The Biological Bulletin 143(1)*: 184-95. https://doi.org/10.2307/1540338

Maple TL and Lindburg DG 2008 Empirical zoo: Opportunities and challenges to research in zoos and aquariums. *Special Issue of Zoo Biology 27(6)*: 431-504. https://doi.org/10.1002/zoo.20214

Margulis SW and Westhus EJ 2007 Evaluation of different observational sampling regimes for use in zoological parks. *Applied Animal Behaviour Science 110*: 363-376. https://doi.org/10.1016/j.applanim.2007.05.001

Martin KJ, Alessi SC, Gaspard JC, Tucker AD, Bauer GB and Mann DA 2012 Underwater hearing in the loggerhead turtle (*Caretta caretta*): a comparison of behavioral and auditory evoked potential audiograms. *Journal of Experimental Biology 215(17)*: 3001-3009. https://doi.org/10.1242/jeb.066324

Mellen J and MacPhee MS 2001 Philosophy of environmental enrichment: Past, present, and future. *Zoo Biology 20*: 211-226. https://doi.org/10.1002/zoo.1021

Mellen JD and Ellis S 1996 Animal learning and husbandry training. In: Kleinman DG, Allen ME, Thompson KV, Lumpkin S and Harris H (eds) *Wild Mammals in Captivity: Principles and Techniques* pp 88-99. University of Chicago Press: Chicago IL, USA

Murphy-Hopkins SR, Owens DW and Murphy TM 2003 Ecology of immature loggerheads on foraging grounds and adults in internesting habitat in the eastern United States. In: Bolten AB and Witherington BE (eds) *Loggerhead Sea Turtles* pp 79-63. Smithsonian Institution Press: Washington, DC, USA

Newberry RC 1995 Environmental enrichment: increasing the biological relevance of captive environments. *Applied Animal Behaviour Science 44*: 229-243. https://doi.org/10.1016/0168-1591(95)00616-Z

Ogden JC, Robinson L, Whitlock K, Daganhardt H and Cebula R 1983 Diel foraging patterns in juvenile green turtles (*Chelonia mydas*) in St Croix United States Virgin Islands. *Journal of Experimental Marine Ecology 66*: 199-205. https://doi.org/10.1016/0022-0981(83)90160-0

O'Hara J and Wilcox JR 1990 Avoidance responses of loggerhead turtles, *Caretta caretta*, to low frequency sound. *Copeia 2*: 564-567. https://doi.org/10.2307/1446362

Proietti MC, Reisser R and Sechhi ER 2012 Foraging by immature hawksbill sea turtles at Brazilian Islands. *Marine Turtle Newsletter 135*: 4-6

Ryan M, Waters R and Wolfensohn S 2021 Assessment of the welfare of experimental cattle and pigs using the Animal Welfare Assessment Grid. *Animals 11(4)*: 999. https://doi.org/10.3390/ani11040999

Sandøe P and Simonsen HP 1992 Assessing animal welfare: where does science end and philosophy begin? *Animal Welfare 1*: 25-267. https://doi.org/10.7120/09627286.1.3.257

Sazima C, Grossman A and Sazima I 2010 Turtle cleaners: reef fishes foraging on epibionts of sea turtles in the tropical Southwestern Atlantic, with a summary of this association type. *Neotropical Ichthyology 8(1)*: 187-192

Schofield G, Katselidid KA, Dimopoulos P, Panis JD and Hays GC 2006 Behavior analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. *Endangered Species Research 2*: 71-79. https://doi:10.3354/esr002071

Therrien CL, Gaster L, Cunningham-Smith P and Manire CA 2007 Experimental evaluation of environmental enrichment in sea turtles. *Zoo Biology 26*: 407-416. https://doi.org/10.1002/zoo.20145

United States Department of the Interior Fish and Wildlife Service 2013 *Standard permit conditions for care and maintenance of captive sea turtles* p 22. https://www.fws.gov/sites/default/files/documents/seaturtle-standard-conditions-for-care-2019.pdf

Valdivia A, Wolf S and Suckling K 2019 Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. *PLoS ONE 14*: e0210164. https://doi.org/10.1371/journal.pone.0210164

van Dam RP and Diez CE 1997 Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. *Coral Reefs 16*: 133-138. https://doi.org/10.1007/s003380050067

van Dam RP and Diez CE 1998a Home range of immature hawksbill turtles (*Eretmochelys imbricata;* Linnaeus) at two Caribbean islands. *Journal of Experimental Marine Biology and Ecology 220(1)*: 15-24. https://doi.org/10.1016/S0022-0981(97)00080-4

van Dam RP and Diez CE 1998b Caribbean hawksbill turtle morphometrics. *Bulletin of Marine Science 62(1)*: 145-55.

Warwick C, Arena PC, Lindley S, Jessop M and Steedman C 2013 Assessing reptile welfare using behavioral criteria. *In Practice 35(3)*: 123-131. https://doi.org/10.1136/inp.f1197

Watters JV, Margulis SW and Atsalis S 2009 Behavioral monitoring in zoos and aquariums: a tool for guiding husbandry and directing research. *Zoo Biology 28(1)*: 35-48. https://doi.org/10.1002/zoo.20207

Webster M 2008 *Inc Merriam-Webster's Collegiate Dictionary.* Merriam Webster: Springfield, USA

Welfare Quality® 2009 *Welfare Quality® Assessment Protocol for Poultry*. Welfare Quality® Consortium: Lelystad, The Netherlands

Whitham JC and 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

Wilkinson A, Chan H and Hall G 2007 Spatial learning and memory in the tortoise (*Geochelone carbonaria*). *Journal of Comparative Psychology 121(4)*: 412-418. https://doi.org/10.1037/0735-7036.121.4.412

Wilson RP, Shepard ELC and Liebsch N 2008 Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research 4*: 123-137. https://doi.org/10.3354/esr00064

Wood LD, Milton S and Maple TL 2017 Foraging behavior of wild hawksbill turtles (*Eretmochelys imbricata*) in Palm Beach County, Florida, USA. *Chelonian Conservation and Biology 16(1)*: 70-75. https://doi.org/10.2744/CCB-1242.1

Zug GR, Wynn AH and Ruckdeschel C 1986 Age determination of loggerhead sea turtles, *Caretta caretta*, by incremental growth marks in the skeleton. *Smithsonian Contributions to Zoology 427*: 1-34

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