Going to the Zoo: Using Tags to Create Measures for Animal Health, Well-being and Welfare in a Managed Care Setting

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Submitted to Swansea University in fulfilment of the requirements for the Degree of Doctor of Philosophy in Biological Sciences

Swansea University

2022

Summary

This PhD investigates how animal-attached motion-sensitive electronic tags might create behavioural biomarkers for animal ‘state’. Such biomarkers could indicate good health, disease, and injuries as well as positive and negative affective states. Success could have widespread implications for the well-being of numerous species in managed care by optimising welfare practices. This work primarily involved loggerhead sea turtles, *Caretta caretta*, in different states of health at the Arca del Mar rehabilitation centre, Oceanogràfic, Valencia, Spain, however the potential of tags for various aquatic, aerial and terrestrial species is also considered. Initially, the concept of tag-derived behavioural biomarkers for health (TDBBs) was established, examining data from ‘healthy’ and ‘unhealthy’ rehabilitating sea turtles to identify potentially useful metrics for specific injuries and/or diseases. Then, potential TDBBs for ‘healthy’ turtles and those with gas emboli were created, with variance in body attitude, number of 45° turns per hour and mean angular velocity per hour showing the most promise to differentiate the two groups. TDBBs were also explored for welfare, giving ‘healthy’ turtles nutritional enrichment, demonstrating that enrichment procedures do not always affect captive animal behaviour. To consider welfare implications of captivity, the movement behaviour of free-living and managed-care loggerheads was compared to determine wild-type and captive behaviour overlap. Findings revealed significant differences in the variance in pitch, heading and absolute angular velocity as well as the number of turns per hour. The final research topic considered trajectory step length data (the distances travelled in between turns), derived from tags deployed on nine wild species, for informing enclosure size for captive animals. The findings revealed that existing enclosure size guidelines regularly only permitted animals to undertake a very small percentage (often less than 3 %) of the step lengths recorded from free-living conspecifics. Last, the potential of TDBBs is reviewed, with limitations and future research discussed.

Declarations and Statements

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed [redacted] (candidate)

Date 15/06/2022

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed [redacted] (candidate)

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I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

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Date 15/06/2022

Funding and Contributing Authors

The work presented in this thesis was funded by Swansea University and the Fundación Oceanogràfic, Valencia, Spain.

In addition to the candidate, Alexandra C. Arkwright, submitting this thesis, the following people and institutions contributed to work undertaken as part of this thesis:

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Author Contributions to Published Work

Chapter 2, which is titled ‘Behavioural biomarkers for animal health: a case study using animal-attached technology on loggerhead turtles’ was published in the Frontiers in Ecology and Evolution journal, in the Behavioural and Evolutionary Ecology section. Author contributions are as follows (initials correspond to names in table on the previous page):

- Experimental conception and design: ACA, EA, AF and RPW.
- Data collection: ACA, EA, AF, VMC and JLC-P.
- Data analysis: ACA, AF, MDH, RMG and RPW.
- Manuscript preparation: ACA, AF and RPW.
- All authors contributed to manuscript revision, read, and approved the submitted version.
- The candidates’ contribution was approximately 90 %; the remaining authors total contribution combined was approximately 10 %.

Contents

Acknowledgements

Firstly, I would like to thank Prof. Rory Wilson at Swansea University and Dr Andreas Fahlman at the Oceanogràfic aquarium, Valencia for creating this PhD opportunity and for giving me the chance to do it justice. My profound thanks go to Andreas Fahlman for his willingness to help day in, day out and for going above and beyond what I could have hoped for when moving to a new country.

Further, I would like to extend my gratitude and appreciation to all staff at the Oceanogràfic, who together run a tight ship and who have made this research possible. In particular I'd like to thank all work experience students and the tirelessly enthusiastic veterinary staff, especially Jose Luis Crespo-Picazo and Vicente Cabedo for teaching me how to handle the turtles, for helping me attach the tags and for notifying me each time a new turtle arrived! Thank you also to those who worked alongside me in the investigation department, especially Andreas Fahlman, Audra Ames and Alicia Borque for creating a lovely working environment, and a big thank you to Silvia Tecles for helping with all things admin-related and more!

Next, I'd like to thank the team at Swansea University: Mark Holton for patiently answering all of my emails (no matter what time of day or night) and working diligently to help not just me but everyone with their tags! What you do is really incredible. Phil Hopkins for fashioning made-to-measure tag housings – again, not just for me but for everyone! And Rich, Lloyd, Jim, Baptiste, Sophie, Alice, Prof. Emily Shepard, plus everyone else who has formed/forms part of the SLAM labs rich tapestry, for being warm and welcoming even though I was often just passing through. I am most grateful to my supervisor Prof. Rory Wilson, without his continued support and guidance throughout this project I would have faltered endlessly. Thank you for always bringing humour, positivity, zest and passion to all that you do; before this PhD, working with such a charismatic and renowned animal behaviour scientist was beyond my wildest dreams! Thank you also to my second supervisor, Prof. Garcia De Leaniz for stepping in and offering a fresh perspective as well as valuable input.

Last, I'd like to thank everyone, supervisors, colleges, friends, and family for being so supportive, patient and understanding. Thank you to Josella (read: mermaid twin and partner in madness) for alerting me to this PhD opportunity and for being a source of great joy in my life. Thank you to Vianney for being my biggest cheerleader, for always endeavouring to make me laugh and for putting up with me even when I'm being unbearable. And special thanks to my mum, who has read through every piece of work I've ever pushed her way and has always encouraged me to do my best.

So, here's my PhD, somewhat later than I'd hoped, but written nonetheless!

Figures and Tables

List of figures and tables, including a summary for each and their location within the text.

Abbreviations

List of abbreviations and what they stand for.

Abbreviation	***Full form***
2D	Two-dimensional
3D	Three-dimensional
AAV	Absolute Angular Velocity
Acc	Acceleration
AIC	Akaike Information Criterion
ALDFG	Abandoned, Lost, Discarded Fishing Gear
BIAZA	British and Irish Association of Zoos and Aquariums
CCL	Curved Carapace Length
CCW	Curved Carapace Width
cf.	Compare
CI	Confidence Interval
$CSL_{50\%}$	Critical Step Length taken at the 50 % limit of the cum. freq. distribution of 'SL' –see below
$CSL_{90\%}$	Critical Step Length taken at the 90 % limit of the cum. freq. distribution of 'SL' –see below
Cum. freq.	Cumulative frequency
CZA	Central Zoo Authority
DA	Dynamic Acceleration
DAVP	Differential Angular Velocity about the Pitch axis
DAVR	Differential Angular Velocity about the Roll axis
DAVY	Differential Angular Velocity about the Yaw axis
DBA	Dynamic Body Acceleration
DCS	Decompression sickness

DD	Daily Diary
DDMT	Daily Diary Movement Trace
DF	Degrees of Freedom
DTAGS	Digital Acoustic Recording Tag
EAZA	European Association of Zoos and Aquaria
G	Gauss
GE	Gas Emboli
GLMM	Generalised Linear Mixed-Effects Model
ICC	Intraclass Correlation Coefficient
ID	Identification
Inf.	Infinity
IUCN	International Union for Conservation of Nature
LMEM	Linear Mixed-Effects Model
Mag	Magnetometry
Mg	MilliGauss
mG/LSB	MilliGauss per Least Significant Bit
MLEs	Maximum Likelihood Estimators (the ‘α_cp’ and the ‘γ’ of a bent-cable model –see below)
MRI	Magnetic Resonance Imaging
N_2	Nitrogen
O_2	Oxygen
ReMI	*Realisable Movement Index* (a tool for assessing animal enclosure size adequacy in zoos, calculated: enclosure length/ ‘SL’ distance at the ‘$CSL_{50\%}$’ or the ‘$CSL_{90\%}$’ limit –see below)
$ReMI_{CSL\_50\%}$	*Realisable Movement Index* calculated using the ‘$CSL_{50\%}$’ –see above
$ReMI_{CSL\_90\%}$	*Realisable Movement Index* calculated using the ‘$CSL_{90\%}$’ –see above
RMU	Regional Management Unit
SCL	Straight Carapace Length
SCSD	Squared Circular Standard Deviation

SD	Standard Deviation
SE	Standard Error
SL	Step Length (the straight-line distance travelled by an animal in between turning points)
TAG	Taxon Advisory Group
TBC	To Be Confirmed
TDBBs	Tag-Derived Behavioural Biomarkers
TDRs	Time Depth Recorders
TEDs	Turtle Excluder Devices
TP	Turn(ing) Point
VeDBA	Vectoral Dynamic Body Acceleration
vs	*Versus*
WAZA	World Association of Zoos and Aquariums
α_cp	Alpha change point (the inflection point in a bent-cable model)
α_rc	Alpha rate constant (the rate of decay exponential curve fits)
γ	Gamma (the half width of the transition zone of a bent-cable model)

Chapter 1

1. Introduction

1.1 Brief taxonomy and life history of sea turtles

Sea turtles (superfamily Chelonioidea) are slow-growing and long-lived reptiles (Wyneken 2003) that arose about 110 million years ago (Figure 1 (Spotila 2004)). There are seven extant species; the loggerhead, *Caretta caretta*, the Kemp's Ridley, *Lepidochelys kempii*, the olive ridley, *Lepidochelys olivacea*, the hawksbill, *Eretmochelys imbricata*, the flatback, *Natator depressus*, the green turtle, *Chelonia mydas* and the leatherback, *Dermochelys coriacea* (Spotila 2004). All share a characteristic morphology, a shell or carapace made of fused ribs and all species alive today are 'hard shelled' except the leatherback which has a 'leathery' or 'soft shell' (Wyneken 2003).

The group has a complex life history that encompasses a diversity of ecosystems from terrestrial coastal habitats, i.e., nesting beaches, where oviposition and embryonic development occur, to developmental areas in the open ocean, (termed the oceanic zone), and mating and foraging habitats in coastal waters (the neritic zone) (Bolten 2003). During the oceanic, developmental phase, often referred to as the 'lost years', turtles remain in oceanic waters and consume epipelagic prey (Carr 1986, 1987; Bjorndal et al. 2000; Snover 2002). Juveniles spend more than a decade in the open ocean before returning to neritic waters to mature and reproduce (Bjorndal et al. 2000; Snover 2002; Bolten 2003). This shift from oceanic to neritic waters is reversible, however, with some individuals moving between coastal waters and the open ocean for reasons that remain unclear (Witzell 2002; Hatase et al. 2006; Hawkes et al. 2006; McClellan & Read 2007).

In a world that is constantly modified by human activities, these ontogenetic habitat shifts can have profound consequences for survivorship (Olson 1996; Turner Tomaszewicz et al. 2017). As a result of their life history, sea turtles are exposed to many location-dependent threats, including beach development, urbanization and light pollution on land (Spotila 2004; Lutcavage 2017), fisheries bycatch, entanglement and ingestion of debris at sea (Tomás et al. 2002; Casale et al. 2010; Nada & Casale 2011).

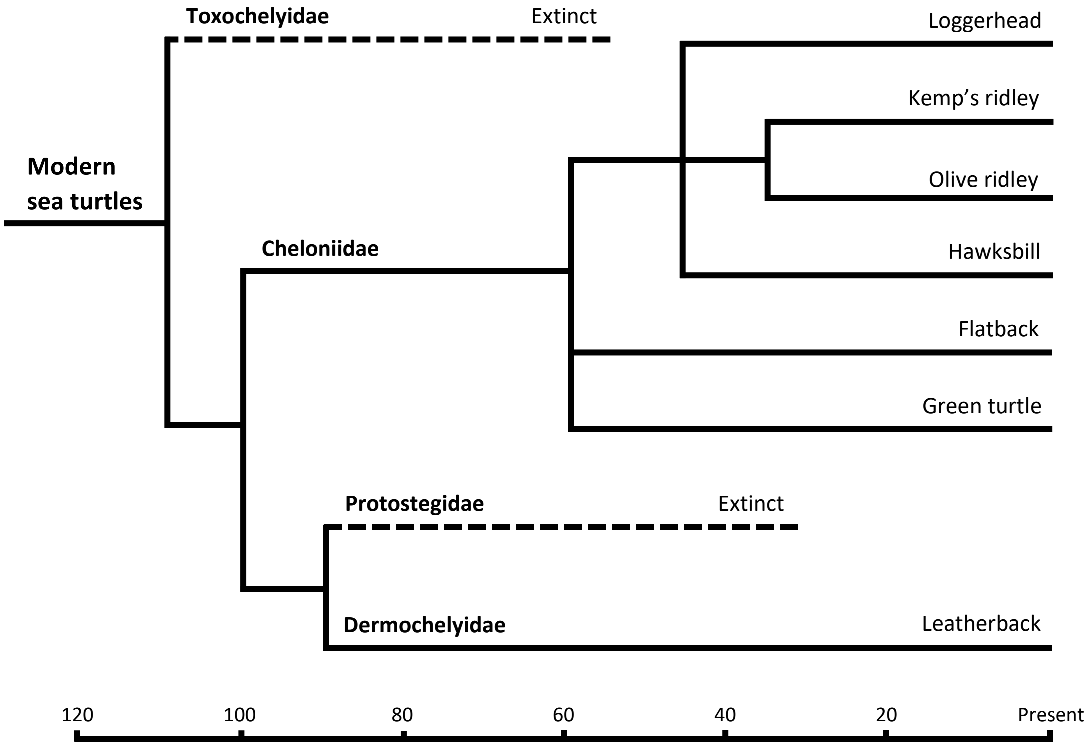

Figure 1. Phylogeny depicting the evolution of modern marine turtles (left to right) which arose from a common ancestor some 110 million years ago. The time scale at the bottom indicates when new forms arose according to the fossil record. Four families of sea turtle are known to have existed, two of which (the Toxochelydae and the Protostegidae) gave rise to very large sea turtle species that are all now extinct. All seven species of marine turtle alive today belong to either the Cheloniidae (hard-shelled turtles) or the Dermochelidae (leathery, soft-shelled turtles). They are descended from a common ancestor about 95 million years ago and are all that remain of the many marine turtle species that once inhabited the Earth's waters. Diagram redrawn from Spotila (2004).

1.2 The loggerhead, *Caretta caretta*

The loggerhead is the sole study species for four of the five research chapters of this PhD. They are so named because of their large, broad head, reaching widths of ~28 cm in adults, and powerful jaws (Pritchard & Mortimer 1999). They have a reddish-brown coloured carapace that is broadest anteriorly, and tapers posteriorly (Figure 2). There is some location-specific variation in adult size, with larger individuals in the north-western Atlantic, reaching straight carapace lengths (SCL) of ~105 cm and the smallest adults in the Mediterranean reaching ~90 cm SCL (Pritchard & Mortimer 1999). Adults in the western Atlantic and off Australia can reach weights of ~180 kg and ~150 kg respectively, whereas Mediterranean adults are usually under 100 kg (Pritchard & Mortimer 1999).

Photography by Alejandro Usategui

Figure 2. Loggerhead turtle with the characteristic reddish-brown carapace that is broadest anteriorly, and tapers posteriorly. The turtle has a Daily Diary tag (DD) that is attached to the second central scute of its carapace using a two-part epoxy.

Of the seven species of sea turtle, the loggerhead is the most widespread, being found in the temperate, subtropical and, less frequently, tropical waters (Figure 3) of all oceans (Tiwari & Bjorndal 2000). Similarly, most nesting beaches are found in subtropical and temperate areas including southeast USA, Oman, temperate Japan, Australia, South Africa, eastern and southern Mediterranean and southern Brazil (Pritchard & Mortimer 1999). Fewer occur in the tropics (Belize and Colombia) and tropical islands, like New Caledonia and the Solomon Islands (Pritchard & Mortimer 1999). Its abundance and widespread distribution, with many nesting beaches located in nations like the USA, Australia, Brazil and the northern Mediterranean, have resulted in the loggerhead becoming both the most tagged (Hays & Hawkes 2018) and most studied marine turtle species (Arendt et al. 2013; Reece et al. 2013).

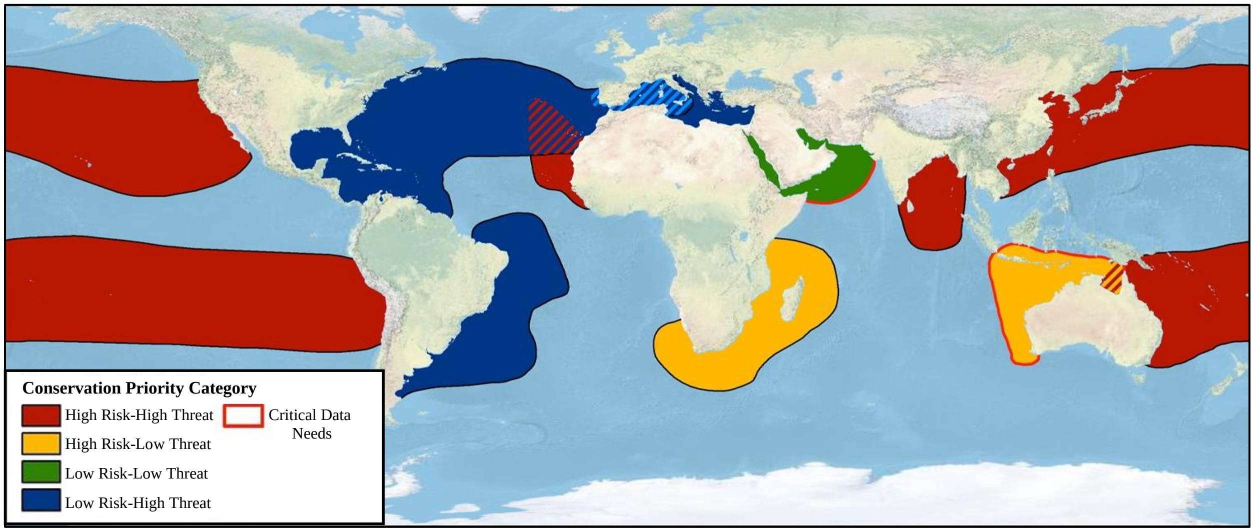

Figure 3. Conservation priority regional management units, RMUs, for loggerhead turtles, extracted from Wallace et al. (2011).

Different loggerhead populations vary not only with respect to their morphology, but also reproductive traits such as egg size, clutch size and nest dimensions (Tiwari & Bjorndal 2000). For example, egg diameter is typically 39–43 mm, while mean clutch size ranges from 90–110 eggs in Mediterranean rookeries to 100–130 elsewhere (Pritchard & Mortimer 1999). This variation may result from different selective pressures at nesting sites, foraging areas and along migratory routes (Tiwari & Bjorndal 2000). Importantly, differences between populations highlight the need for regional conservation in order to protect genetic and phenotypic variation (Buskirk & Crowder 1994; Tiwari & Bjorndal 2000; Carreras et al. 2007). Furthermore, developmental changes in behaviour, habitat and resource use (Bjorndal et al. 2000; Snover 2002; Bolten 2003) expose loggerheads to a host of hazards (see section 1.3) and have important implications for measures intended to protect them from both coastal and open-ocean sources of mortality (McClellan & Read 2007).

1.3 Threats, conservation and research

Sea turtles are of conservation concern (Frazier 2005; Peckham et al. 2007; Mancini et al. 2011; Schofield et al. 2013), being threatened across their entire distribution by many anthropogenic and natural hazards. Human-induced threats include over-exploitation *via* illegal egg harvesting (Madrigal-Ballestero & Jurado 2017; Mejías-Balsalobre et al. 2021), collisions with boats and entanglement in fishing nets or other marine debris (Tomás et al. 2002; Casale et al. 2010). In addition, most nesting beaches, especially those around the Mediterranean, have been degraded as a result of urbanisation and resort development (Margaritoulis et al. 2003; Lopez et al. 2015). This has increased the levels of light pollution, noise and traffic that both nesting females and hatchlings encounter (Margaritoulis et al. 2003; Spotila 2004). Turtles also face a large number of natural threats to hatching success: microbial infection (Bézy et al. 2015; Gambino et al. 2020), storms and inundation of nesting beaches (Peters et al. 1994; Pike & Stiner 2007; Fuentes et al. 2010), lethal sand temperatures (Matsuzawa et al. 2002; Valverde et al. 2010) and highly skewed female to male ratios (Jensen et al. 2018) resulting in reduced fertility levels (*cf.* Miller et al. 2003; Phillott & Godfrey 2020). It has been estimated that 1 in 1,000 eggs survive to adulthood (Frazer 1986).

Three of the seven sea turtle species are listed as vulnerable in the International Union for Conservation of Nature (IUCN 2022) Red List of Threatened Species; loggerheads (Casale & Tucker 2017), olive ridleys (Abreu-Grobois et al. 2008), and leatherbacks (Wallace et al. 2013). The remaining species are under greater threat, being considered endangered (green turtles; (Seminoff 2004)) and critically endangered (hawksbills and Kemp ridleys; (Mortimer et al. 2008; Wibbels & Bevan 2019)) or are lacking sufficient data for an evaluation to be made (flatbacks; (Red List Standards & Petitions Subcommittee 1996)). Recent subpopulation assessments of green turtles, however, have downgraded their threatened status from endangered to least concern (South Atlantic subpopulation: Broderick & Patricio 2019) and vulnerable (North Indian Ocean subpopulation: Mancini et al. 2019). Furthermore, published estimates of sea turtle population sizes worldwide indicate that the majority are increasing, showcasing how conservation efforts and increased data collection (see section 1.3.1) are helping populations recover globally (Mazaris et al. 2017; Valdivia et al. 2019; Ceriani et al. 2019).

Ever-growing awareness and enthusiasm for turtle protection, combined with increased research and management effort, has resulted in numerous conservation projects (especially at nesting beaches (Bradford & Israel 2004; Campbell & Smith 2006; Chan 2013; Nahill 2021)), countless rehabilitation centres (Stevens 2019; Stelfox et al. 2021), and a plethora of published scientific work on marine turtle biology and ecology (Avise 2007; Campbell 2007; Campbell & Cornwell 2008; Hamann et al. 2010; Piovano et al. 2011; Stringell et al. 2015). Since the first nesting site-based projects appeared (dating back to the 1950s at some locations (Troëng & Rankin 2005; Nel et al. 2013)), their number has increased dramatically, with many hundreds of conservation projects in operation worldwide (Frazier & Bache 2002). Work carried out by these projects is invaluable to identify research priorities relating to nest site selection, reproductive biology and effective conservation strategies (Hamann et al. 2010; Wallace et al. 2011).

1.3.1 Sea turtle conservation: roles of nesting beach projects and rehabilitation centres

Sea turtles are increasingly used as flagship species for conservation (Tisdell & Wilson 2003). Being highly charismatic, sea turtles can be used as ambassadors for a variety of environmental causes (Eckert & Hemphill 2005; Frazier 2005) providing an effective way of introducing the general public to marine conservation (Blumenthal et al. 2006). Nesting beach projects and rehabilitation centres are well placed to educate people of all ages, raising awareness through volunteer opportunities, by admitting visitors (Ballantyne et al. 2007; Feck & Hamann 2013), tracking sea turtle migrations online and working with the local media/press (Richardson et al. 2010). These activities encourage community engagement and also generate revenue which can then fund other projects. Well established nesting beach projects provide a platform from which to branch out from rookery conservation to the sea where incidental capture and entanglement are frequently identified as major sources of mortality (James et al. 2005; Wallace et al. 2010). Satellite tracking has revealed where turtle-fishery interactions represent a threat to species, helping to inform spatial and temporal restrictions on fisheries to aid population recovery (James et al. 2005; Wallace et al. 2010; Stringell et al. 2015; Jeffers & Godley 2016).

Today, nesting beaches are where most sea turtle conservation interventions are carried out (Schroeder & Murphy 1999; Hamann et al. 2010), with interventions ranging from methods to improve hatching success, (e.g., hatcheries, predator deterrents, nest protection, nest relocation, shading, tree planting and watering (Tomillo et al. 2007; Longo et al. 2009; Patino-Martinez et al. 2012; Esteban et al. 2018; Shaver 2020)) to more recent efforts to minimise light pollution (Lara et al. 2016; Colman et al. 2020) and mitigate against the effects of climate change (Strange et al. 2011; Tomillo et al. 2015; Esteban et al. 2018; Smith et al. 2021). Such conservation strategies work to boost hatchling and adult female survival, thus helping to reverse declining trends in over-exploited populations when implemented over the course of a couple of decades or more (Mortimer & Bresson 1994; Dutton et al. 2005; Broderick et al. 2006; Chaloupka et al. 2008; Stokes et al. 2014). Studies reporting rising population numbers at a number of locations demonstrate the success of these measures (Hays 2004; Arendt et al. 2013; Stokes et al. 2014; Piacenza et al. 2016; Mazaris et al. 2017; Valdivia et al. 2019; Ceriani et al. 2019; Laloë et al. 2020).

While long-term records from flipper tagging of nesting turtles have been instrumental in documenting population trends (Bjorndal et al. 1999; Hays 2004; Arendt et al. 2013; Stokes et al. 2014; Piacenza et al. 2016; Casale et al. 2018; Ceriani et al. 2019), efforts to raise awareness have encouraged many members of the public to support sea turtle conservation and rehabilitation by volunteering, making donations, paying for turtle tours/experiences and purchasing merchandise (Tisdell & Wilson 2000b; Shanker & Pilcher 2003; Chan 2010; Ballantyne et al. 2011; Chan 2013; Feck & Hamann 2013; Silva et al. 2016). In addition, nesting beach projects and rehabilitation centres are uniquely placed to encourage cooperation and effective working relationships between managers, scientists, the public and the government (Piniak & Eckert 2011; Mestre et al. 2014; Baker et al. 2015; Silva et al. 2016; Fahlman et al. 2017; Arkwright et al. 2020). Aside from the obvious conservation and scientific benefits, sea turtle projects can also have a positive socio-economic effect, *via* job creation and education (Marcovaldi & Marcovaldi 1999; Buitrago et al. 2008; Ferraro & Gjertsen 2009; Silva et al. 2016). Furthermore, in areas with indigenous people, many projects have worked to create sustainable harvesting programs, thus reducing poaching and enabling resource users to continue their traditional lifestyle (Eckert & Hemphill 2005; Grayson et al. 2010; Butler et al. 2012; Silva et al. 2016). Local involvement can also lead to community-based monitoring (Whiting et al. 2006; Pilcher & Chaloupka 2013), beach cleans (Cheng 2007; Martin 2013) and bottom-up pressure on governments as locals seek legislation for community reserves (Peckham et al. 2007).

Despite the prolonged conservation efforts, public awareness and scientific interest, some sea turtle populations remain in decline or have still to recover to pre-exploitation levels (Wallace et al. 2011; Mazaris et al. 2017). In the wake of several decades of beach protection, the marine realm is perhaps where the greatest threats to sea turtle survival are currently found.

1.3.2 Marine threats: entanglement and bycatch

Entanglement in fishing gear poses a serious threat to sea turtles (Wilcox et al. 2013; Nelms et al. 2015; Stelfox et al. 2016) with entrapment resulting in both restricted movement and growth and causing injuries ranging from abrasions to flipper loss. Furthermore, the increased drag resulting from attached gear also hampers foraging ability and may cause death *via* starvation and drowning (Barreiros & Raykov 2014). Severe injuries may leave rehabilitators with no alternatives other than flipper amputation and euthanasia (Barreiros & Raykov 2014). In some cases, sea turtles may never be fit for re-release, thus increasing the burden on rehabilitation centres (Baker et al. 2015). There is also a trend towards larger life stages (adults and sub-adults) being recorded as bycatch (Santos et al. 2012). This is of great concern since, as a long-lived, slow-maturing species, the loss of adults has huge repercussions for population growth and stability. One study in northern Australia found that sea turtles made up 80% of the animals caught in 5,491 ghost-nets (Wilcox et al. 2013). While it may be that abandoned, lost, discarded fishing gear (ALDFG) chiefly impacts adult foraging/breeding habitats and migration routes, smaller turtles maybe able to escape through finer mesh sizes and given their size would decompose more quickly making them less likely to be found (Nelms et al. 2015).

Large juvenile loggerheads tracked by satellite, have been found foraging in shallow waters (as expected) as well as in the open ocean (McClellan & Read 2007), demonstrating the importance of both neritic and oceanic environments for juveniles. Indeed, large juveniles are regularly bycaught in pelagic longline fisheries in oceanic waters (Watson et al. 2005). Although sea turtle bycatch can be somewhat mitigated through the use of Turtle Excluder Devices (TEDs) in trawl fisheries (Brewer et al. 2006; Vasapollo et al. 2019), loggerheads that spend protracted periods in the ocean are threatened by largely unregulated international fisheries e.g., the pelagic swordfish and tuna longlines (Lewison et al. 2004; Gilman 2011; Chan & Pan 2016). Satellite tracking does, however, reveal prime foraging sites and migratory pathways (Godley et al. 2002; Godley et al. 2008) and this information can be used to inform and help implement fishery regulations (Fitzgerald et al. 2004; Blumenthal et al. 2006; Snoddy & Williard 2010; Stringell et al. 2015). Furthermore, at locations where turtles and fisheries come into regular contact, rehabilitation centres may provide vital support for populations by treating animals with a variety of bycatch-related diseases and injuries (Baker et al. 2015; Innis et al. 2019). They also play an important role in returning turtles to the ocean where they can contribute to the next generation (Caillouet et al. 2016).

1.3.3 Sea turtle rehabilitation facilities

Wildlife rehabilitation (i.e. releasing sick, injured and orphaned animals back into the wild after treatment) as a form of conservation and a method of stabilizing and augmenting wild populations, is growing in popularity (Karesh 1995; Cardona et al. 2012; Mestre et al. 2014). The principal driver behind the movement to rehabilitate marine megafauna is concern for the welfare of individual animals: in the past such individuals were destined to remain in human controlled environments indefinitely (Moore et al. 2007). Although the number of rehabilitated individuals is generally too small to affect wild populations significantly (Moore et al. 2007; Quakenbush et al. 2009), except perhaps in the case of birds after oil spills (Wolfaardt et al. 2009), rehabilitation centres can play an important role in informing and galvanizing society. For example, releasing rehabilitated animals back into the wild creates opportunities for media events, which can be used to inform, apply political pressure on decision-makers, and even help enforce conservation measures, further extending the conservation value of rehabilitation efforts (Moore et al. 2009; Baker et al. 2015).

In fact, making people aware of the threats to sea turtles and changes that people can make in their lives to minimize them may have a greater impact on restoring turtle numbers than rehabilitation alone (Feck & Hamann 2013). Surveys distributed at a number of Australian rehabilitation facilities revealed that, following their visit, people were willing to make changes in their lives to help protect turtles and even donate annually to sea turtle conservation (Feck & Hamann 2013). Furthermore, visitors to Mon Repos Conservation Park indicated in follow-up surveys that they made changes to their everyday lives, like picking up rubbish, taking more care with waste disposal and not using plastic bags, as a result of their visit (Ballantyne et al. 2011). People respond to viewing injured wildlife up close and are more motivated to change their behaviour and donate money, as demonstrated by visitors to turtle nesting beaches (Wilson & Tisdell 2001; Tisdell & Wilson 2003; Ballantyne et al. 2011). Allocating this additional income to funding conservation and research to manage threats can help mitigate the threats sea turtles face (Tisdell & Wilson 2000a, b; Feck & Hamann 2013). Furthermore, the economic value of sea turtles can also attract legal support, such as enforcing ‘go slow zones’ and other fishery restrictions (Wilson & Tisdell 2001; Peckham et al. 2007).

1.3.3.1 Rehabilitation costs and limitations

Rehabilitation centres often depend on external funding from governments, donations from the public and organisations, and visitor entrance fees to generate income (Feck & Hamann 2013). This money goes towards rehabilitation costs, i.e., medical care, facility and equipment up-keep and paying staff, in particular veterinary surgeons (Feck & Hamann 2013). Sea turtle rehabilitation regularly takes months, if not years, depending on the seriousness of the illness or injury, so centres need to be able to house multiple individuals at once (Cardona et al. 2012). While the rehabilitation costs per sea turtle appear not to have not been published, they could reach several thousand dollars, although this is like to vary greatly between individuals and locations (Feck & Hamann 2013). It is also important to note that most of the animals admitted to rehabilitation centres only require aid following adverse interactions with anthropogenic hazards such as fishing nets and boats (Tribe & Brown 2000; Tomás et al. 2002; Dutton & Squires 2008; Casale et al. 2010; Bagarinao 2011; Feck & Hamann 2013).

Despite all of the work and costs that go into supporting rehabilitation centres, not much is known about the likelihood of survival or success in post-release animals (Caillouet et al. 2016; Innis et al. 2019) although such information is of clear value (Karesh 1995; Tribe & Brown 2000). A prime limitation for the few studies that have tracked animals after release is the associated expense (Cardona et al. 2012; Mestre et al. 2014; Innis et al. 2019). So, to date, most of the available evidence is anecdotal or drawn from small sample sizes. Nonetheless, some behavioural abnormalities have been reported in ‘head-started’ (the process of rearing sea turtles in captivity during their most vulnerable period (Burke 2015)) (Swingle et al. 1994; Addison & Nelson 2000) and rehabilitated sea turtles (Addison & Nelson 2000; Bellido et al. 2010), as well as in other rehabilitated marine vertebrates (Anderson et al. 1996; Nawojchik et al. 2003; Mazzoil et al. 2008; Thomas et al. 2010). For example, one study which compared the behaviour of six rehabilitated loggerheads with 12 healthy turtles (captured and released in the same region), found that rehabilitated turtles travelled faster, differed in their turning behaviour, spent more time at the surface at night and had a higher percentage of shelf use (Cardona et al. 2012). These behavioural anomalies could be legacies of the illnesses and injuries sustained prior to rehabilitation or may be the culmination of a prolonged stay in captivity.

Against this, some studies have found no difference between captive-raised and wild loggerhead dispersal patterns (Polovina et al. 2006) and both loggerhead and green turtles have been found to migrate towards known foraging sites post-rehabilitation (Mestre et al. 2014). There is also evidence that wild-born sea turtles maintain their ability to navigate and forage in the open ocean even after long-term stays in captivity; this ability was observed in a wild-caught loggerhead turtle that successfully completed a return migration to natal beaches along the Japanese coastline after being held in captivity in Mexico for 10 years (Nichols et al. 2000). Despite these encouraging small-scale studies, our understanding of the effect of captivity on post-release turtle behaviour is minimal.

Given that rehabilitation has substantial financial costs, it is important to understand the success rates of treated animals. In many cases, rehabilitation success may be low; between 1999–2010 records from Queensland, Australia showed only 26 % of stranded sea turtles found washed up on beaches were successfully rehabilitated and re-released (StrandNet; compiled from Haines &

Limpus 2000; Haines & Limpus 2001; Greenland et al. 2004; Greenland & Limpus 2006, 2008; Biddle & Limpus 2011). Moreover, a study reviewing 1,700 sea turtle admissions to rehabilitation centres in Florida (USA) from 1986–2004 found that 61.5% died in rehabilitation and a further 1.6% were kept in captivity due to the severity of their injuries (Baker et al. 2015). The same study found that larger individuals were most likely to be successfully rehabilitated and that loggerheads had the best survival chances, followed by Kemp's ridley and then green turtles (Baker et al. 2015).

Given that rehabilitation may have a limited potential when it comes to counterbalancing turtle bycatch (particularly in heavily fished areas such as the western Mediterranean), perhaps the most important role for these facilities is within society (section 1.3.3) and for data/sample collection purposes (Cardona et al. 2012). A major advantage to maintaining and treating animals in captivity is the potential to educate whilst creating memorable human-wildlife interactions and in doing so, increase awareness and support for important causes (Tribe & Brown 2000; Moore et al. 2007; Cardona et al. 2012; Feck & Hamann 2013). Consequently, the social benefits combined with the direct benefits to wildlife, may justify the cost and time it takes to rehabilitate individual animals (Baker et al. 2015).

1.3.4 Research at rehabilitation facilities

Rehabilitation facilities are regularly involved in research covering a board range of topics including;

(i) socio-economic issues relating to public awareness, public support for a given cause and financial gain (Tribe & Brown 2000; Moore et al. 2007; Richardson et al. 2010; Feck & Hamann 2013)

(ii) conservation matters, such as investigating which sea turtle species and age groups are most at risk (Baker et al. 2015; Innis et al. 2019) and

(iii) tagging rehabilitated individuals to assess survival (Cardona et al. 2012) and behaviour (Addison & Nelson 2000; Nichols et al. 2000; Bellido et al. 2010; Cardona et al. 2012) post-release.

Moreover, because rehabilitation centres around the world admit turtles suffering a wide range of injuries, they could be instrumental in illuminating areas of high mortality, often caused by fishery related incidents (James et al. 2005; Polovina et al. 2006; Dutton & Squires 2008; Casale et al. 2010; Bagarinao 2011; Stringell et al. 2015; Casale & Tucker 2017). Pinpointing hazardous areas facilitates implementation of location-specific regulations such as spatial and temporal restrictions on fisheries (Wallace et al. 2010; Stringell et al. 2015; Jeffers & Godley 2016) and 'go slow' zones (Wilson & Tisdell 2001; Peckham et al. 2007).

In addition to injured turtles, rehabilitation centres admit diseased individuals, a combination creating unique opportunities for veterinary science. Published manuscripts reveal that turtles are susceptible to diseases including fibropapillomatosis (Croft et al. 2004; Page-Karjian et al. 2014), various fungal infections (Cabanes et al. 1997; Manire et al. 2002; Oros et al. 2004), parasitic marine leeches (Köhnk et al. 2021) and gas emboli (also known as decompression sickness) (García-Párraga et al. 2014; Fahlman et al. 2017; Portugues et al. 2018). Importantly, rehabilitation centres can play vital roles in raising awareness through reporting case numbers (Maier 2004; Casal & Orós 2009), establishing suitable medical procedures (Cabanes et al. 1997; Greer et al. 2003; Croft et al. 2004; Arencibia et al. 2012; García-Párraga et al. 2014), and investigating factors linked to or causing injury/disease (Maier 2004; Fahlman et al. 2017).

There is a real need to be able to diagnose specific injuries and diseases (Melvin et al. 2021) as well as assess captive turtle well-being (Burghardt et al. 1996; Burghardt 2013; Arena et al. 2014), (particularly for animals requiring long or indefinite stays in captive care) in a timely and effective manner. This is especially true during winter months when turtle admissions tend to be higher and rehabilitation centres are under greater strain (García-Párraga et al. 2014; Roberts et al. 2014; Niemuth et al. 2020). During such periods, standardized procedures facilitating rapid diagnosis, treatment and continued assessments to ensure that animals are receiving optimal care, could ease the pressure on rehabilitation centres whilst speeding up animal recovery and improving survival chances post-release. One way of achieving this may be to deploy motion- and orientation-sensitive tags on rehabilitating turtles to investigate whether animal movement (which is synonymous with behaviour (Tinbergen 1960, 1963)) can be used as an indicator of specific health conditions (see: Broom & Johnson 1993; Rushen 2003; Lawrence 2008).

Multi-sensor tags, despite having been used extensively to quantify free-living animal behaviour and study the ecology of threatened megafauna (Wilson et al. 2008; Fossette et al. 2010; Sleeman et al. 2010; Brown et al. 2013; Wilson et al. 2013a; Wilson et al. 2013b; Bidder et al. 2015; Wilson et al. 2016; Wilson et al. 2017; Wilson et al. 2020), have seldom been used to examine and quantify the behaviour of captive animals (but see: Ropert-Coudert et al. 2009; Thorup et al. 2015; Shorter et al. 2017). Deployments on wild animals showcase ever expanding ways for assessing behaviour and state (Shepard et al. 2006; Shepard et al. 2008; Wilson et al. 2008; Shepard et al. 2013; Wilson et al. 2014; Walker et al. 2015; Williams et al. 2015; Péron et al. 2017; Williams et al. 2017; Wilson et al. 2018; Williams et al. 2020; Munden et al. 2021) that could be applied to the study of animals in rehabilitation and other captive settings.

Since behaviour can indicate condition (Broom & Johnson 1993; Rushen 2003; Boissy et al. 2007; Lawrence 2008; Nathan et al. 2008; Scollo et al. 2014; Benn et al. 2019), changes in health during an animals recovery are likely to be reflected behaviourally, i.e., *via* specific movement and body attitudes (Wilson et al. 2008; Guesgen & Bench 2017; Shorter et al. 2017; Arkwright et al. 2020). If condition-dependent behavioural traits can be reliably detected and quantified *via* animal-attached devices, sensor technology may offer a novel and systematic way of assessing animal health and monitoring recovery remotely (Thorup et al. 2015). In addition, such frameworks might be transferable to the study of animal well-being in zoos and aquariums. Using this thinking, during this PhD I investigated the potential of tagging technology to determine the health and well-being of sea turtles in rehabilitation, with a view to showcasing the methods that could potentially transform the operational procedures adopted by rehabilitation and captive care centres. I also sought to demonstrate how tags used on a variety of wild animals give critical data on movement patterns and how consideration of these could help us create animal-appropriate enclosures, allowing a sufficient percentage of free-living animal movement patterns to be undertaken.

1.4 PhD Chapters

This PhD is divided into seven chapters, an introduction (above– Chapter 1), five research chapters written in the format of scientific papers, and a synopsis chapter.

The second chapter introduces the concept of using animal-attached electronic technology on sea turtles in managed care to assess the viability of producing metrics that define and assess turtle condition, i.e., health status. This concept is based on the idea that healthy individuals will move differently to unhealthy animals and that these differences will be determinable and quantifiable *via* animal-attached devices recording data from a suite of sensors, such as accelerometers, magnetometers, and depth sensors (tagging technology is discussed at length in Chapters 2 and 5 and does not feature extensively within the introduction to avoid repetition). In essence, the chapter examines the variation within data streams recorded by the tag sensors according to individual condition and specifically compares behavioural data from 'healthy' and 'unhealthy' rehabilitating sea turtles to identify potentially useful metrics, termed tag-derived behavioural biomarkers (TDBBs), that could be indicative of specific injuries and/or diseases. The work is supported by, and makes use of, established veterinary procedures undertaken at the rehabilitation centre to ground the investigation. The chapter raises important questions such as 'Is behaviour indicative of health status?' whilst also exploring which behavioural elements might be most useful for diagnostic purposes and case follow-up.

The third chapter takes a more in-depth look at TDBBs related to decompression sickness. This condition (caused by dissolved gases coming out of solution and forming bubbles within the body upon depressurization (Francis & Gorman 1993; Francis & Mitchell 2002; Vann et al. 2011)), was first documented in sea turtles by García-Párraga et al. (2014). Until recently, it was believed that diving marine vertebrates, unlike human divers, were resistant to such pressure-dependent illnesses (Lemaitre et al. 2009), but it is now known to be prevalent in bycaught sea turtles (Fahlman et al. 2017; Portugues et al. 2018). The chapter considers metrics that showed potential for defining this condition, including turtle activity, manifest by dynamic body acceleration– DBA, specifically VeDBA (Qasem et al. 2012), turn rate, body pitch and body roll.

An issue closely related to animal health is animal welfare, especially where zoos and aquariums are concerned (Boissy et al. 2007; Mellor & Beausoleil 2015; Bashaw et al. 2016; Benn et al. 2019). Surprisingly though, the use of tagging technology to investigate animal welfare at these venues has been relatively unexplored. Chapters 4 and 5 centre on this to ascertain whether animal-attached tags may form practical animal welfare assessment tools. For captive animals, environmental enrichment is reported to play a major part in improving and maintaining a high standard of animal welfare (Shyne 2006; Bacon 2018). Often, enrichment is food-related, i.e., through the provision of moving prey or some kind of problem-solving challenge before feeding can take place (Lyons et al. 1997; Knowles & Plowman 2001; Jenny & Schmid 2002; Bashaw et al. 2003). Chapter 4 looks at how nutritional enrichment, by way of feeding experiments with moving and stationary prey, may affect sea turtle behaviour both during, and in the hours following ingestion. However, the work showed that prey type only affected two out the twelve different movement metrics (heading variance and the number of 180º turns). I discuss the importance of monitoring behaviour to assess whether a given type of enrichment has the expected or desired impact.

Chapter 5 continues the topic of animal welfare, comparing the behaviour of free-living loggerheads with that of managed care animals in; (i) barren rescue centre tanks and (ii) structurally diverse aquarium exhibits. The goal was to assess the extent to which wild-type and captive behaviour, (assessed by a variety of different movement metrics including VeDBA, angular velocity and turn extent) overlapped between the three scenarios.

Understanding the behavioural plasticity of free-living animals could help improve the quality of life for conspecifics in captive care as well as help improve welfare standards if wild animals could be compared with captive individuals. My final research chapter utilises free-living animal movement path data, specifically the constellation of species-specific straight-line distances travelled during normal movement, to create a science-based approach for guiding minimum space requirements and enclosure sizes for captive animals. Capitalising on high-resolution movement path data from a variety of aerial, terrestrial and aquatic free-living animals, I propose a ‘Realisable Movement Index’, *ReMI*, a novel method that could provide guidance on adequate enclosure sizes.

The final chapter of this body of work is a synopsis that explores some other findings that emerged whilst doing this work, as well as some of the difficulties I faced. I also discuss avenues for further research.

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Chapter 2

Behavioural biomarkers for animal health: a case study using animal-attached technology on loggerhead turtles

Published in: Frontiers in Ecology and Evolution, 2020.

Citation: Arkwright AC, Archibald E, Fahlman A, Holton MD, Crespo-Picazo JL, Cabedo VM, Duarte CM, Scott R, Webb S, Gunner RM. 2020. Behavioural biomarkers for animal health: a case study using animal-attached technology on loggerhead turtles. *Frontiers in Ecology and Evolution* **7**:504.

Abstract

Vertebrates are recognized as sentient beings. Consequently, urgent priority is now being given to understanding the needs and maximizing the welfare of animals under human care. The general health of animals is most commonly determined by physiological indices e.g., blood sampling, but may also be assessed by documenting behaviour. Physiological health assessments, although powerful, may be stressful for animals, time-consuming and costly, while assessments of behaviour can also be time-consuming, subject to bias and suffer from a poorly defined link between behaviour and health. However, behaviour is recognized as having the potential to code for stress and well-being and could, therefore, be used as an indicator of health, particularly if the process of quantifying behaviour could be objective, formalized and streamlined to be time efficient. This study used Daily Diaries (DDs), (motion-sensitive tags containing tri-axial accelerometers and magnetometers), to examine aspects of the behaviour of bycaught loggerhead turtles, *Caretta caretta* in various states of health. Although sample size limited statistical analysis, significant behavioural differences (in terms of activity level and turn rate) were found between 'healthy' turtles and those with external injuries to the flippers and carapace. Furthermore, data visualization (spherical plots) clearly showed atypical orientation behaviour in individuals suffering gas emboli and intestinal gas, without complex data analysis. Consequently, we propose

that the use of motion-sensitive tags could aid diagnosis and inform follow-up treatment, thus facilitating the rehabilitation process. This is particularly relevant given the numerous rehabilitation programs for bycatch sea turtles in operation. In time, tag-derived behavioural biomarkers, TDBBs for health could be established for other species with more complex behavioural repertoires such as cetaceans and pinnipeds which also require rehabilitation and release. Furthermore, motion-sensitive data from animals under human care and wild conspecifics could be compared in order to define a set of objective behavioural states (including activity levels) for numerous species housed in zoos and aquariums and/or wild species to help maximize their welfare.

1. Introduction

Animals are recognized as cognizant beings, with high priority now given to understanding behavioural requirements and maximizing animal welfare under human care (Hawkins 2004; Boissy et al. 2007; Shorter et al. 2017). Generally, animal well-being is evaluated through physiological health assessments e.g., periodic blood sampling, which can cause animals distress and pain (Abou-Ismail et al. 2007; Burman et al. 2007; Scollo et al. 2014) whilst also being expensive and time consuming (Hawkins 2004). However, animal health can also be assessed through behaviour, requiring an understanding of differing behavioural states that result from factors like elevated stress, infirmity, and injury (Broom & Johnson 1993; Rushen 2003; Lawrence 2008). At present, assessments of behaviour can be time-consuming, subject to bias and suffer from a poorly defined link between behaviour and well-being in general (Broom & Johnson 1993; Rushen 2003; Lawrence 2008). Animal-attached technology may thus provide a solution to many of these issues, enabling the process of quantifying behaviour to be formalized and streamlined to be time-efficient and objective (Cooke et al. 2004; Ropert-Coudert & Wilson 2005; Ellwood et al. 2007; Cooke 2008; Guesgen & Bench 2017).

The attachment of tags to animals, which started decades ago (as early as the 1960s in marine vertebrates (Kooyman 2004)), has transformed our understanding of animal behaviour and ecophysiology (Naito 2004) and catalysed the development of whole new disciplines such as movement ecology (Nathan et al. 2008). In particular, archival-, rather than transmission-tag technology (also known as biologging, where multiple parameters are recorded (Ropert-Coudert & Wilson 2005)), has demonstrated its use in helping transform our understanding of animal physiology (Block 2005; Sherub et al. 2017), behaviour (Brown et al. 2013) and ecology (Wilmers et al. 2015). Biologging also has huge potential in areas relating to animal well-being *via* studies on farmed animals, particularly cattle (Turner et al. 2000; Shirai & Yokoyama 2014; Thorup et al. 2015), but also aquaculture (Andrewartha et al. 2015) and with respect to conservation (Cooke 2008; Ropert-Coudert et al. 2009; Bograd et al. 2010; Wilson et al. 2015a). Accelerometer biologgers have also proved valuable for tracking behavioural changes and the survival of various fish species (including blacktip sharks, *Carcharhinus limbatus* (Whitney et al. 2016)*;* arapaima, *Arapaima cf. arapaima* (Lennox et al. 2018) and bonefish, *Albula spp.* (Brownscombe et al. 2013) post-release, following fishery-related and recreational capture. For farmers, tagging has a wide range of applications from locating animals that have escaped their paddocks and tracking resource consumption (Sikka et al. 2006), to detecting lameness (Thorup et al. 2015)– activities which would usually require manpower and time. Recently biotelemetry has also gained popularity within pet caring practices with dog owners tracking their pets to know their whereabouts (Mancini et al. 2012).

Somewhat surprisingly, given the clear potential of biologging to monitor animal health, the tagging community has done relatively little work in zoos and aquariums (with the exception of some studies that have used animals under human care to help identify behaviours with a view to using loggers on wild animals (Shepard et al. 2008; Ismail et al. 2012). One notable study that does, however, report on the potential of logging technology to study the well-being of animals under human care, is that by Shorter et al. (2017), which examined the activity of a total of ca. 57 h of data derived from 5 bottlenose dolphins, *Tursiops truncatus*, using motion-sensing animal-attached tags (DTAGS, see Johnson and Tyack (2003)). Another study, on koalas at a conservation centre, used accelerometers in combination with electrocardiogram recorders to assess heart rate during periods of inactivity whilst animals where in the presence and absence of tourists (Ropert-Coudert et al. 2009). Otherwise, the lack of tags on animals maintained in a controlled environment *per se* is particularly curious since tags are unlikely to be lost (Bidder et al. 2014), animals are easy to catch compared to their wild counterparts and can even be trained to participate voluntarily (Ward & Melfi 2015; Shorter et al. 2017). Moreover, the issue of animal welfare is repeatedly raised within the context of zoos and aquariums (Hill & Broom 2009). Indeed, many of the major issues discussed relating to animal welfare, such as the incidence of stereotypic behaviours (Mason & Rushen 2008), stress (Wiepkema & Koolhaas 1993) and assessing the extent to which behaviours exhibited by animals under human care conform to those of their wild conspecifics (Veasey et al. 1996), could potentially be well quantified by logger technology (Wilson et al. 2014; Pagano et al. 2017).

A decade ago, a multi-sensor archival tag, the ‘Daily Diary’, DD, (which records tri-axial acceleration and tri-axial magnetometry, temperature and pressure) was conceived to quantify the behaviour and ecology of threatened megafauna (Wilson et al. 2008). However, this tool has not been used, until now, to elucidate the link between animal behaviour and health (Broom & Johnson 1993; Rushen 2003; Lawrence 2008). Since behavioural state should relate to biomarkers of stress and well-being, the DD has the potential to be used to derive metrics which act as ‘behavioural biomarkers’ of health (Broom 1991; Lawrence 2008) and form part of a less invasive diagnosis process (requiring no physiological samples).

The present study used DD loggers to examine aspects of the behaviour of bycaught loggerhead turtles, *Caretta caretta*, housed in the ‘Arca del Mar’ rehabilitation centre at the Oceanogràfic aquarium, Valencia, Spain. Sea turtles being rehabilitated at the centre commonly suffer bycatch-related external and/or internal injuries, including gas emboli (i.e., the formation of gas bubbles within the blood stream and tissues) and decompression sickness (Portugues et al. 2018). No animal was caught for the purpose of this study. The aim of this study was to investigate whether tag-derived ‘behavioural biomarkers’ (TDBBs) for health could be established by monitoring changes in movement behaviours determined by multi-sensor tags and validated through conventional health assessments during sea turtle rehabilitation. We hypothesized that specific behavioural aspects would vary in accordance with a particular illness/injury, thus enabling the creation of TDBBs that could then be used to track recovery and potentially serve as diagnostic tools. This article also discusses how data from motion- and orientation-sensitive animal-attached tags might be used to derive useful metrics (such as activity level and turning rate) for assessing animal health and welfare in human controlled environments.

2. Method

2.1 Animals

All of the loggerhead turtles used in this study were accidentally captured (bycaught) in gillnet and trawling fisheries off the coast of eastern Spain except potentially: three that were found floating at the surface, two that were transferred from other aquariums and one that was found stranded (see Table 1). Sea turtles were brought to the facility by staff from the local strandings network; the duration from the point of accidental capture to arriving at the centre was not known. All bycaught turtles from participating fishing boats were brought to the clinic even if the animal did not exhibit visible signs of disease or trauma. Sea turtles were typically brought to the centre with a variety of bycatch-related external and/or internal injuries including gas emboli and decompression sickness (García-Párraga et al. 2014; Portugues et al. 2018).

2.2 Veterinary care

Clinical examination was carried out at the rehabilitation centre, 'Arca del Mar' which is managed by the Fundación Oceanogràfic in Valencia, Spain. The facility has a permit from the Valencian Regional Government for sea turtle rehabilitation (both bycaught and stranded) and post-mortem examination. Upon arrival, all turtles underwent a health assessment including a complete physical examination, blood sample collection and diagnostic imaging (radiographs and ultrasound). Vets used turtle entry number (a running count of the number of turtles admitted year on year) to identify individuals; for ease the same identification numbers were used in this manuscript. Turtle numbers were preceded by a 'T' to help differentiate them from other numbers within the text.

Table 1. Summary of tagged turtles including turtle identification number, entry to and release dates from the rehabilitation centre, bycatch origin, weight (kg) (curved carapace length, CCL and curved carapace width, CCW, provided in Appendix A), cause of injury/disease (when known) and the animals' state of health upon entry and on the date of tagging (as deduced via veterinary examination). NB: gas emboli (GE) was categorised as mild, moderate or severe; turtles that entered with GE were considered 'convalescent' when tagged within a couple of days of admission as they were only released into holding tanks following hyperbaric chamber treatment and once there was no sign of GE in the blood.

Turtle ID	**Entry**	**Release**	**Origin**	**Weight (kg)**	**Cause of injury/ disease**	**State of health upon entry**	**Tagging date**	**State of health when tagged**
297	03/01/17	22/08/17	Cullera	5.4	Trawl/ bottom fishing	Severe GE, died and was resuscitated	17/04/17	Healthy
308	16/02/17	30/06/17	Calpe	10	Trawl/ bottom fishing	Moderate GE	18/04/17	Healthy
318	15/03/17	20/04/17	Cullera	3.5	Trawl/ bottom fishing	Moderate GE	18/04/17	Healthy
320	17/03/17	21/04/17	Peniscola	9.47	Trawl/ bottom fishing	Mild-Moderate GE	18/04/17	Healthy
322	23/03/17	21/04/17	Peniscola	5.55	Trammel net	Drowned, died and was resuscitated	18/04/17	Healthy
324	31/03/17	13/05/17	Valencia	17	Trawl/ bottom fishing	Healthy	29/04/17	Healthy
325	03/04/17	29/04/17	Valencia	11.54	Trawl/ bottom fishing	Healthy	22/04/17	Healthy
326	04/04/17	11/06/17	Gandia	15.5	Trammel net	Drowned, died and was resuscitated	25/04/17	Convalescent
330	12/04/17	06/05/17	Oropesa	5.6	Unknown (found floating at surface)	Healthy	22/04/17	Healthy
331	18/04/17	08/06/17	Gandia	3.07	Trammel net	Intestinal gas, buoyancy issues	22/04/17	Buoyancy issues
332	26/04/17	DIED	San Sebastian	18.9	Unknown (transferred from another aquarium)	Multi-organ failure	29/04/17	Multi-organ failure
339	22/07/17	10/04/18	Benidorm	4.2	Stranded with gillnet associated injuries	Severely damaged and infected right front flipper	29/11/17	Damaged and infected right front flipper
342	11/10/17	TBC*	Vinaroz	15.8	Trawl/ bottom fishing	Severe carapace trauma and damage to spinal cord	15/12/17	Severe carapace trauma and damage to spinal cord

Turtle ID	Entry	Release	Origin	Weight (kg)	Cause of injury/ disease	State of health upon entry	Tagging date	State of health when tagged
343	23/10/17	20/06/18	San Sebastian	11.19	Unknown (transferred from another aquarium)	Buoyancy issues	15/12/17	Buoyancy issues
344	26/09/17	18/12/17	Vinaroz	12.1	Trammel net	Healthy	29/11/17	Healthy
345	02/11/17	20/12/17	Vinaroz	17.1	Trammel net	Healthy	29/11/17	Healthy
347	03/11/17	Euthanised	Murcia	4.52	Unknown, found stranded (transferred from another aquarium)	Carapace trauma, partial front flipper amputation	24/05/18	Carapace trauma, partial front flipper amputation
350	28/11/17	27/12/17	Peniscola	15	Trawl/ bottom fishing	Moderate GE	29/11/17	Convalescent
352	05/12/17	06/06/18	Cullera	4.45	Trawl/ bottom fishing	Severe GE, died and was resuscitated	07/12/17	Bites and skin infection
359	02/01/18	04/03/18	Benicarlo	20.8	Trawl/ bottom fishing	Moderate GE	03/01/18	Convalescent
362	16/01/18	06/03/18	Cullera	13	Trawl/ bottom fishing	Moderate GE	09/02/18	Healthy
380	05/03/18	10/04/18	Calpe	8.4	Trawl/ bottom fishing	Moderate GE	12/03/18	Convalescent
383	14/03/18	14/04/18	Cullera	11.6	Trawl/ bottom fishing	Moderate GE	15/03/18	Convalescent
384	15/03/18	06/04/18	El Saler	15.2	Trawl/ bottom fishing	Mild GE	16/03/18	Convalescent
385	18/03/18	20/07/18	Valencia	8.6	Trawl/ bottom fishing	Healthy	15/06/18	Healthy
393	28/03/18	04/05/18	El Saler	28.71	Trawl/ bottom fishing	Moderate GE	18/04/18	Convalescent
396	28/03/18	05/07/18	Vinaroz	22	Trawl/ bottom fishing	Healthy	08/05/18	Healthy
397	05/04/18	03/06/18	Gandia	7.3	Trammel net	Drowned and was resuscitated	08/05/18	Convalescent
399	06/04/18	08/06/18	Cullera	5.7	Trammel net	Healthy	06/06/18	Healthy
402	16/04/18	09/06/18	Burriana	5.7	Trawl/ bottom fishing	Healthy	29/05/18	Healthy
403	06/05/18	29/06/18	El Perello	7.24	Unknown (found floating at surface)	Healthy	11/06/18	Healthy
404	07/05/18	06/07/18	Almenara	3.24	Unknown (found floating at surface)	Wounded neck	13/06/18	Wounded neck
405	01/06/18	12/07/18	Peniscola	34.24	Trawl/ bottom fishing	Very mild GE	26/06/18	Healthy

Continued.

Sea turtles at the facility were housed in circular tanks, ranging from 2–6 m in diameter and with a water depth of 0.95 m. Two different filtration systems operated maintaining ‘A’ and ‘B’ tanks at temperatures of ~20°C and ~24°C respectively, in order to acclimatize sea turtles to lower temperatures before they were released. All animals admitted were maintained at the rehabilitation centre until they were deemed fit for release.

2.3 Gas embolism and decompression sickness

It has recently been found that some bycaught loggerheads exhibit gas emboli within the blood stream and tissues and suffer symptoms of decompression sickness; afflicted animals have also been found to display anomalous behaviours ranging from being comatose to being hyperactive (García-Párraga et al. 2014). Embolisms can lead to organ injury, impairment, and even animal mortality, especially in individuals with moderate to severe gas emboli that do not receive hyperbaric O_2 treatment (García-Párraga et al. 2014).

The presence and severity of gas emboli were determined by radiographs and ultrasound examination and scored on a 5-point scale: no intravascular gas detected, very mild, mild, moderate and severe (for further details see (García-Párraga et al. 2014; Fahlman et al. 2017)). Animals with observable gas emboli received recompression therapy using pure O_2 from a pressurized medical O_2 cylinder. This hyperbaric oxygen treatment was administered *via* a custom-built hyperbaric chamber (41 cm x 77 cm, internal height and diameter). After recompression treatment (which was often administered overnight due to turtles arriving in the afternoon/evening), another health assessment was conducted to evaluate the resolution of gas emboli. Individuals were only placed in holding tanks once no gas emboli were detected in the blood (usually the morning after recompression treatment) and were considered to be in a state of recovery (convalescent) from that moment on. Turtles remained under daily supervision until their blood values and their feeding, swimming and diving behaviours were normal.

2.4 Tagging

Sea turtle behaviour was studied by equipping animals with acceleration- and magnetic-field-measuring data-loggers (‘Daily Diaries’, DD, housing dimensions 54 x 29 x 22 mm, mass 22 g, although there was some variation in size (Wilson et al. 2008)) recording at 20 Hz per channel. Devices measured both acceleration (logged with respect to gravity (approx. 1 g), range; ± 16 g) and magnetic field intensity (recorded in Gauss (G) at 0.73 mG resolution, range; ± 0.88 G) in three orthogonal axes: heave (dorso-ventral), surge (anterior-posterior) and sway (lateral). In addition to describing behaviour *via* body posture, body ‘vibrancy’ (Halsey et al. 2011b) and body rotation (Williams et al. 2017), tags quantified proxies for energy expenditure (dynamic body acceleration– DBA, specifically VeDBA (Qasem et al. 2012), and the physical characteristics of the animal’s environment, i.e., temperature and pressure (Wilson et al. 2008).

In order to attach the DDs, bycaught turtles were lifted out of their holding tank and placed onto a foam mat and/or into a plastic box. Tags were attached to the second central scute of the carapace with a two-part epoxy (Veneziani Subcoat S), pre-mixed in water. Animals were tagged opportunistically for deployment periods lasting just over a day, up to six consecutive days during April–May and November–May 2017–2018. When possible, turtles were tagged as soon as they were released into one of the holding tanks at the rehabilitation centre. This varied according to condition; for healthy turtles and those with minor injuries, individuals could be admitted to a tank following a veterinary health assessment, whereas for turtles with gas emboli (which typically received hyperbaric treatment overnight), this was usually the day following recompression treatment. All protocols were approved by the Oceanogràfic Animal Care & Welfare Committee (OCE-16-18) and the Swansea University Animal Welfare Ethical Review Body (STU_BIOL_82015_011117151527_1). No medical procedures were conducted solely for research purposes.

2.5 Data analysis

The data were analysed using custom designed software ‘Daily Diary Multi Trace’ (DDMT, http://wildbytetechnologies.com/software.html), R-Studio (version 3.6.0, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/), the R packages ‘nlme’, (version 3.1-141 (Pinheiro & Bates 2000; Pinheiro et al. 2008)) and ‘MuMIn’, (version 1.43.6 (Barton 2013)) and Microsoft Excel (version 365). Data visualization with DDMT displayed sensor lines (tri-axial acceleration, tri-axial magnetic field intensity, pressure, temperature and derivatives– see below) on the y-axis against time on the x-axis as well as multi-dimensional plots that were used to reveal patterns in the data (Walker et al. 2016; Wilson et al. 2016; Williams et al. 2017). These took the form of spherical (tri-axial) plots where two axes (the horizontal axes) displayed two different parameters, such as time and animal body pitch, while the third, vertical, axis displayed a frequency count. This enabled the incidence of particular conditions to be examined easily. Certain parameters, such as pitch and roll, have values that describe a sphere, resulting in frequency histograms forming on the surface of a sphere.

Derivatives used for describing behaviours included the dynamic body acceleration (*DBA*), specifically the vectorial dynamic body acceleration (VeDBA), using methods described in Qasem et al. (2012), because *DBA* is a proxy for both energy expenditure in vertebrates in general (Halsey et al. 2011b) and loggerhead turtles in particular (Halsey et al. 2011a *cf.* Enstipp et al. 2011), as well as being a useful general measure for activity (Gleiss et al. 2011). Another useful derivative when examining animal behaviour is that of compass heading (i.e., orientation about the yaw axis or turning) (Bidder et al. 2015; Walker et al. 2015b; Williams et al. 2017). DDMT software uses calibration data to correct for iron distortions and tilt offsets prior to calculating heading on a scale of 0–360º. Any tilt of the DD causes a distortion in the compass heading values, which are corrected through the use of the static component of acceleration (due to gravity; 9.81 m/s^{-2}), the animal’s pitch and roll values, in relation to the output of the tri-axial magnetometers (Walker et al. 2016); also known as a tilt-compensated compass. For information regarding the stages and equations involved in the computation of pitch, roll and compass heading see Bidder et al. (2015) and Walker et al. (2015b). Subsequent analyses including mean VeDBA per hour and heading (specifically the number of turns per hour surpassing a threshold of 45º) were calculated using data undersampled from 20 Hz to 4 Hz; VeDBA and heading data was also smoothed over two seconds to reduce noise. VeDBA and heading were used in statistical analysis after data visualisations indicated differences in animal movement (pitch, roll and directionality) for turtles in various states of health and because the two parameters combined provided a straight-forward (and therefore easily applicable) but also reasonably comprehensive way of investigating potential differences in movement behaviour.

A linear mixed-effects model (LMEM) was performed to see if turtle condition (included as a predictor) affected the relationship between the number of turns per hour (surpassing a threshold of 45^{o}) and mean VeDBA per hour. A log transform was performed on both the dependent (VeDBA) and independent (turn rate) variables to normalise the data and turtle ID was incorporated into the model as a random effect to account for inter-individual differences (for example, turtle size and sex). Tank size was also included in the model to account for any confounding effects it might have; consequently, the model included all turtles (n = 22) tagged post July 2017 for which tank size (i.e., the available water mass) was known (see Table 1).

In order to perform the analysis, turtle condition was grouped into three categories: healthy (n = 9; used as baseline reference), external injury (n = 5; e.g., skin lesions and flipper and carapace damage) and internal injury (n = 8; e.g., intestinal gas and gas emboli). To account for diurnal changes in behaviour the model contained 24 hours of data per turtle with the analysis starting one hour after each turtle had been released into a tank to allow for acclimatisation post handling. The model was run using the ‘lme’ function in R, from the ‘nlme’ package (Pinheiro & Bates 2000; Pinheiro et al. 2008); to allow for heterogeneity of variance between individuals (indicated by model diagnostic plots) the model was updated to include the ‘varIdent’ function (Gałecki & Burzykowski 2013). Akaike Information Criterion (AIC) values along with forwards stepwise selection were used to find the best fitting model and *p*-values were obtained *via* the ‘anova’ summary. Marginal and conditional R^2 values for model goodness-of-fit were calculated using the ‘r.squaredGLMM’ function in the ‘MuMIn’ package (Barton 2013), (the marginal R^2 indicated the variance explained by fixed factors, and conditional R^2 indicated the variance explained by both fixed and random factors (Nakagawa & Schielzeth 2013). The magnitude of dependence in scores attributable to differences between turtles (turtle ID) was quantified *via* the intraclass correlation coefficient (ICC). This was estimated as proportion of variance in the dependent variable (VeDBA) resulting from turtle ID, to total variance; where σ_{τ}^{2} was the estimated turtle variance and σ_{ε}^{2} was the estimated residual variance (Kenny & Hoyt 2009).

$$ICC = \frac{\sigma_\tau^2}{\sigma_\tau^2 + \sigma_\varepsilon^2}$$

3. Results

Thirty-three turtles were tagged during this study; upon the date of tagging, 17 were considered healthy (based on veterinarian assessments), eight were recovering from various degrees of gas emboli (convalescent), five had external injuries (on the neck, flipper and/or carapace), two had buoyancy issues and one suffered multi-organ failure of unknown causes (see Table 1 for details). Study animals were small to large juveniles, ranging from 30–64 cm, curved carapace length, CCL and weighing between 3.24–34.24 kg. Despite the relatively large sample size, the variation in condition and small number of comparable individuals for condition (especially with respect to correcting for e.g., size and sex) meant that we had little capacity to verify our results statistically; as such we were unable to link specific pathologies with movement data.

Nonetheless, statistical analysis (performed with turtles tagged post- July 2017 for which tank size was known (n = 22; see Table 1)), did indicate that turtle condition (grouped into healthy (n = 9), external injury (n = 5) and internal injury (n = 8)) affected behaviour, specifically the relationship between mean VeDBA and the number of 45$^{\text{o}}$ turns performed per hour (Table 2; Figure 1). Forwards stepwise selection and AIC values showed that the full model incorporating all covariates (turn rate, turtle condition, turtle ID and tank size) yielded the best goodness-of-fit (marginal R^2 = 0.81; conditional R^2 = 0.96). The number of turns per hour (that surpassed 45$^{\text{o}}$) significantly affected VeDBA (LMEM: $\chi^2_{(2)}$ = 143.28, p < 0.001); for every 10% increase in turn rate, VeDBA increased by just over 3% (Est. = 0.33 ± 0.02 (S.E), t = 17.04, 95% CI[0.292, 0.367], p < 0.001). The largest tank size (containing a water volume of 19,000 L) had a significant negative effect on this relationship. External injuries had a significant positive effect on turtle activity; per 10% increase in turn rate, VeDBA increased by almost 2% (Est. = 0.18 ± 0.06 (S.E), t = 3.01, 95% CI[0.052, 0.301], p = 0.01). Internal injuries, however, did not significantly affect the relationship between turn rate and activity (Est. = 0.07 ± 0.054 (S.E.), t = 1.52, 95% CI[-0.025, 0.157], p =

0.15). The intraclass correlation coefficient (ICC) was high (0.98), indicating high similarity between values from the same group (n = 22).

Table 2. Linear mixed-effects model (LMEM) estimates of fixed effects, p-values and 95% confidence intervals for log-transformed VeDBA. The analysis was performed to see if turtle condition (healthy, external injury or internal injury) affected the relationship between the number of turns per hour (surpassing a threshold of 45°) and mean VeDBA per hour during the first 24 hours of tag attachment.

Variable	**Est.**	**S.E.**	***t*-value**	**D.F.**	**95% CI**	***p*-value**
Intercept	-5.06	0.12	-47.04	505	[-5.270, -4.850]	0.00
Log turns/hour (45°)	0.33	0.02	17.04	505	[0.292, 0.367]	0.00
External injury	0.18	0.06	3.01	15	[0.052, 0.301]	0.01
Internal injury	0.07	0.04	1.52	15	[-0.025, 0.157]	0.15
Tank size (3000 L)	-0.05	0.07	-0.69	15	[-0.188, 0.095]	0.50
Tank size (3500 L)	0.01	0.06	0.16	15	[-0.120, 0.140]	0.87
Tank size (6000 L)	-0.14	0.06	-2.09	15	[-0.273, 0.001]	0.05
Tank size (19000 L)	-0.19	0.07	-2.87	15	[-0.335, -0.051]	0.01

3.1 Movement patterns for various conditions

Raw acceleration data showing movement patterns for turtles in varying states of health indicated differences at the individual level and in relation to condition (Figures 2 and 3) although more data are needed to be able to have the statistical power to determine this. A period of initial heightened activity was apparent in all example turtles (except T332) and ranged from half an hour to three hours (see Figure 2, individuals T402 and T384 respectively) or more (see Figure 3, individuals T350 and T359). Acceleration data together with depth (pressure) data showed that turtles generally exhibited alternating active and rest periods (with rest periods at the bottom of the tank typically lasting 10–15 minutes). This behaviour was most clearly defined in healthy turtles. Rest periods in turtles recovering from gas emboli (T383 and T384) were less distinguishable (as the acceleration traces were not as smooth) and more erratic. Magnetometry data, (indicating animal orientation) changed closely in accordance with acceleration movement in healthy example turtles and individuals recovering from gas emboli (Figure 3). The trace that differed most from the others was that of T332 with multi-organ failure (Figure 2) that died soon after tagging. The turtle remained at the surface and moved little (as indicated by the elevated depth trace remaining constant and the small spikes in the VeDBA trace compared to the other turtles respectively; Figure 2).

3.2 Activity over time

As observed previously, VeDBA (activity) in all healthy and unhealthy turtles (except T332 with multi-organ failure) was markedly raised for the first three to four hours (Figure 4), particularly in animals with gas emboli (Figure 4b). After this initial period, VeDBA values tended to remain low and constant ($< 0.05\ g$) although some infirm individuals exhibited erratic periods of higher and lower VeDBAs (see Figure 4, individuals T331 and T384 in particular and Figure 5). The mean VeDBA for healthy turtles and standard deviation (Figure 4) were calculated using the seven turtles considered free of both disease and injury upon admission (despite 17 being considered healthy on the date of tagging) due to the subtle or undetectable long-term damage that gas emboli (particularly severe cases) can cause. During the first 24 hours of tagging the VeDBA values of most afflicted turtles were within one standard deviation of healthy ones. However, the two rehabilitating turtles that deviated most frequently (T342 and T347) had both suffered severe carapace traumas (the latter also had a damaged fore flipper). Consistently low VeDBA values were recorded for T342, whereas for T347 they were within the healthy turtle range for the first 12 hours and then rose markedly above but in parallel with a small hump in VeDBA observed in healthy turtles some 20 hours post-tagging.

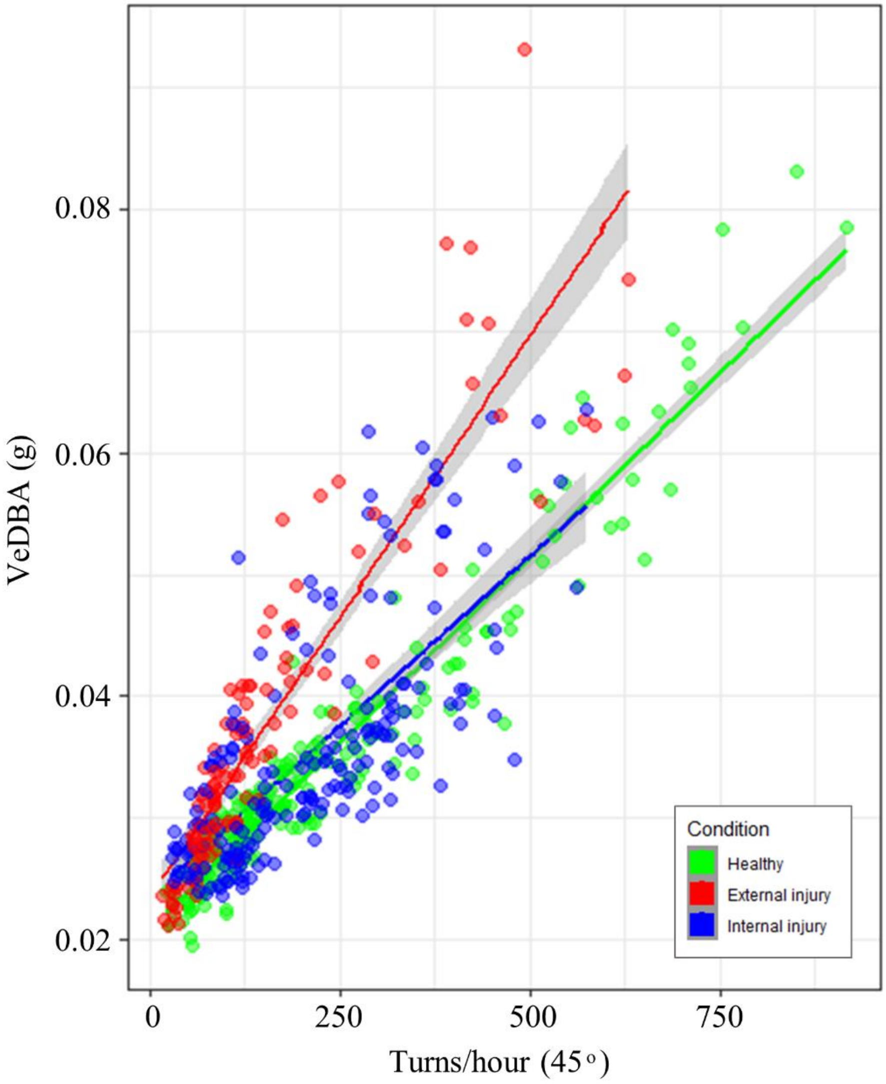

Figure 1. Relationship between the number of turns per hour that surpassed a 45° threshold and mean VeDBA (g) per hour. Data points and regression lines are colored according to turtle condition (healthy = green, external injury = red and internal injury = blue); 95% confidence intervals are indicated by the gray shading either side of regression lines. Line gradients indicate that the relationship between turning rate and VeDBA differed little between healthy turtles and those with internal injuries; turtles with external injuries however, had substantially higher VeDBA values per number of turns.

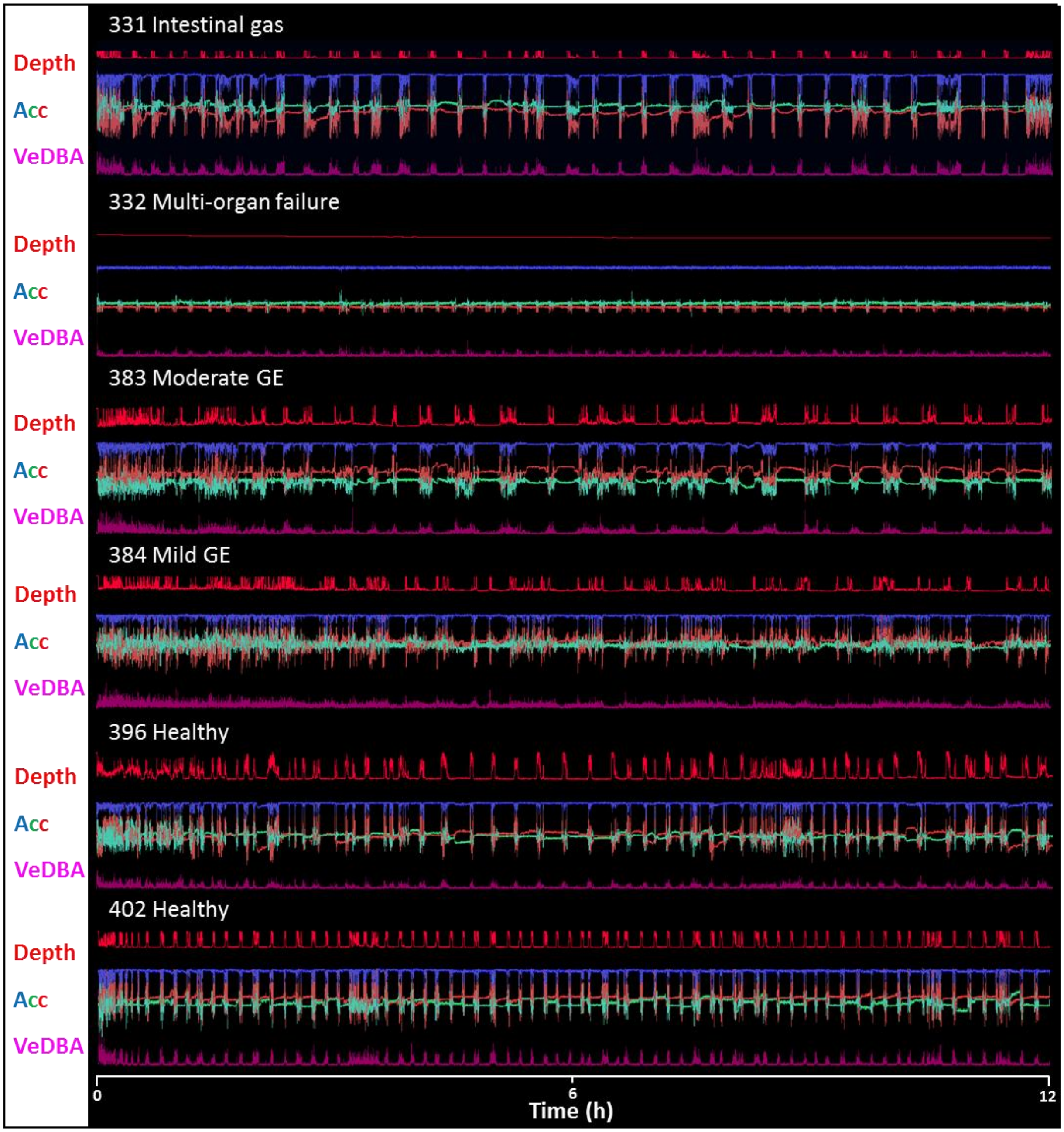

Figure 2. Daily Diary recordings for five different individuals in various conditions showing depth (dives are readily apparent), the three orthogonal acceleration channels (Acc) and a general activity metric (VeDBA– for definition see text). Scale is omitted to declutter graph, but acceleration limits are -1–1 g, and the depth limit is ca. 1 m). Data show 12 hours from the first time a turtle was tagged. Note how traces vary with animal condition, in particular individual T332 with multi-organ failure that, unlike the other individuals, did not exhibit regular, alternating rest and dive periods. Most animals displayed increased activity at first, that decreased with time; this was most evident in animals with GE where an initial period of 2–3 hours of high activity was visible (cf. Figure 3).

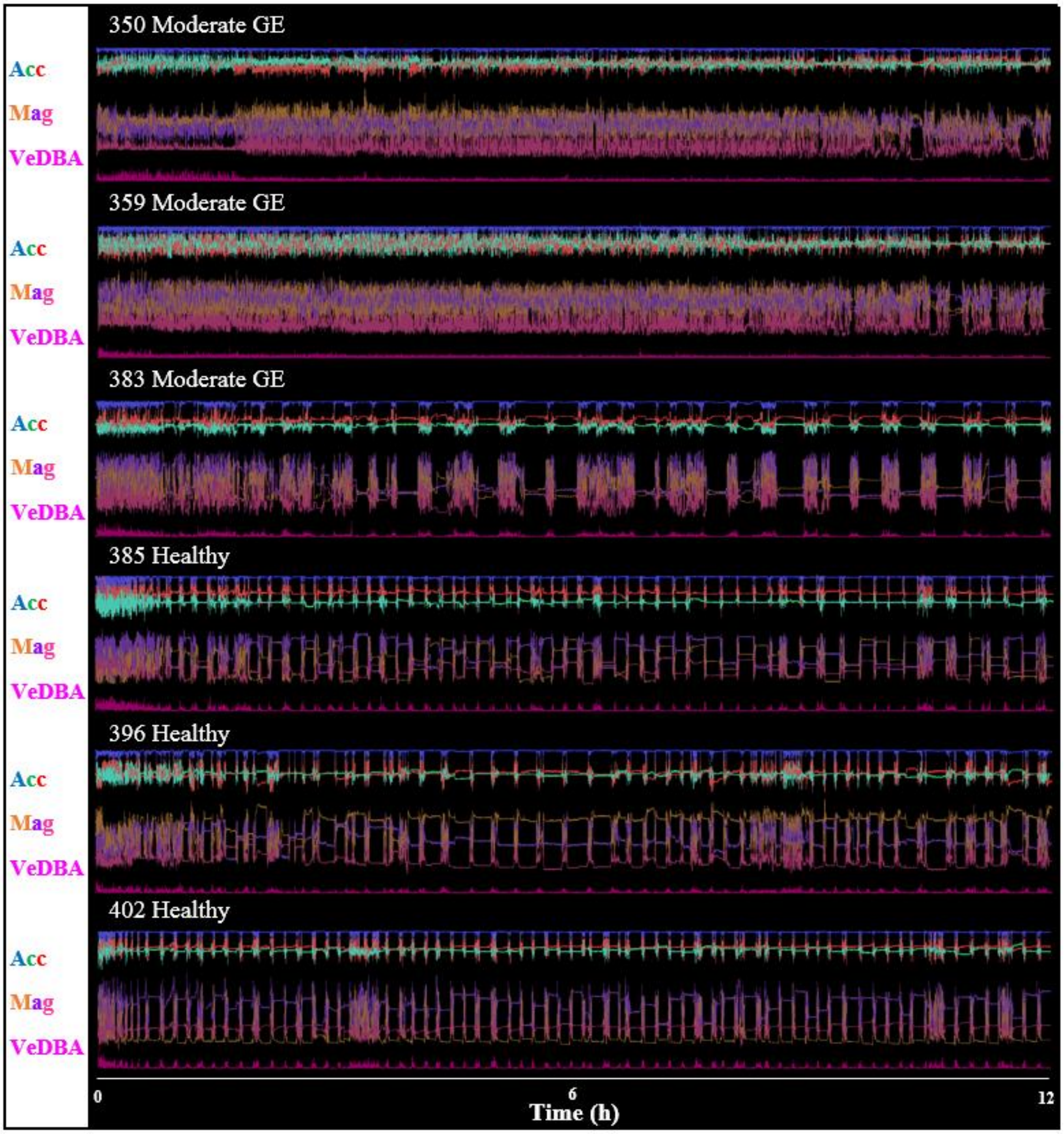

Figure 3. Daily Diary recordings for six different individuals in various conditions showing the three orthogonal acceleration channels (Acc), three magnetometry channels (Mag) and a general activity metric (VeDBA– for definition see text). Scale is omitted to declutter graph; acceleration limits are -1–1 g, magnetometry limits 0.2–0.8 G). Data show 12 hours from the first time a turtle was tagged. Note how traces vary between individuals that are healthy and those with GE; the former tended to display regular, alternating rest and dive periods, exhibited by the magnetic field data, and the latter exhibited increased activity lasting three hours or more.

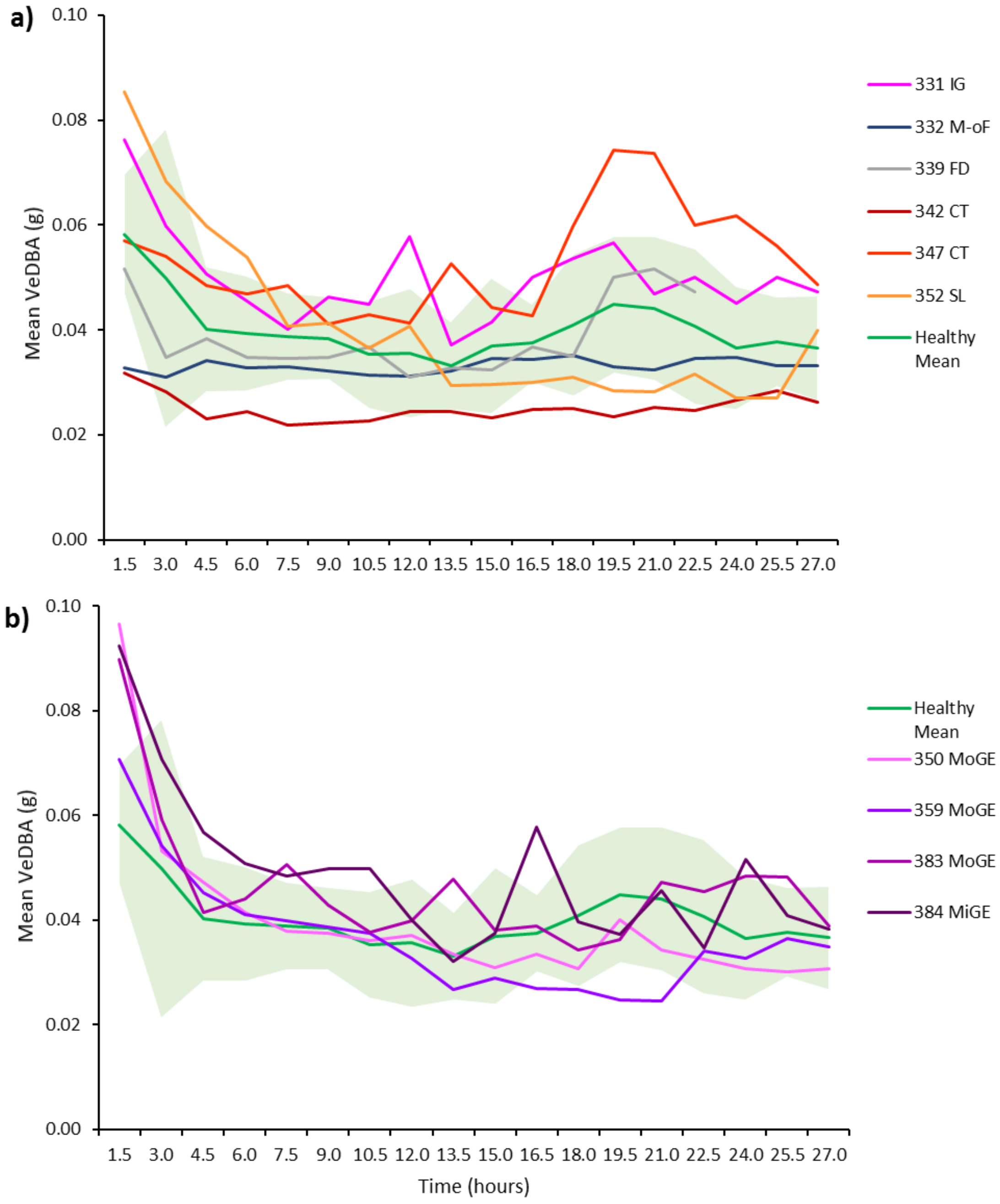

Figure 4. Changes in VeDBA (activity) over time in turtles with (a) various diseases and injuries and (b) turtles with GE, from the first moment they were tagged (cf. Figures 1 and 2). Turtles are identified by number (see Table 1). Abbreviations indicate condition: IG = intestinal gas, M-oF = multi-organ failure, FD = flipper damage, CT = carapace trauma, SL = skin lesions, MoGE = moderate gas emboli and MiGE = mild gas emboli. The mean VeDBA of turtles that were considered healthy upon entry (individuals 324, 325, 330, 344, 345, 385 and 396) is shown in green; the shaded light green area represents one standard deviation. Note the initially high values observed in most turtles for the first three to four hours (particularly in animals with GE).

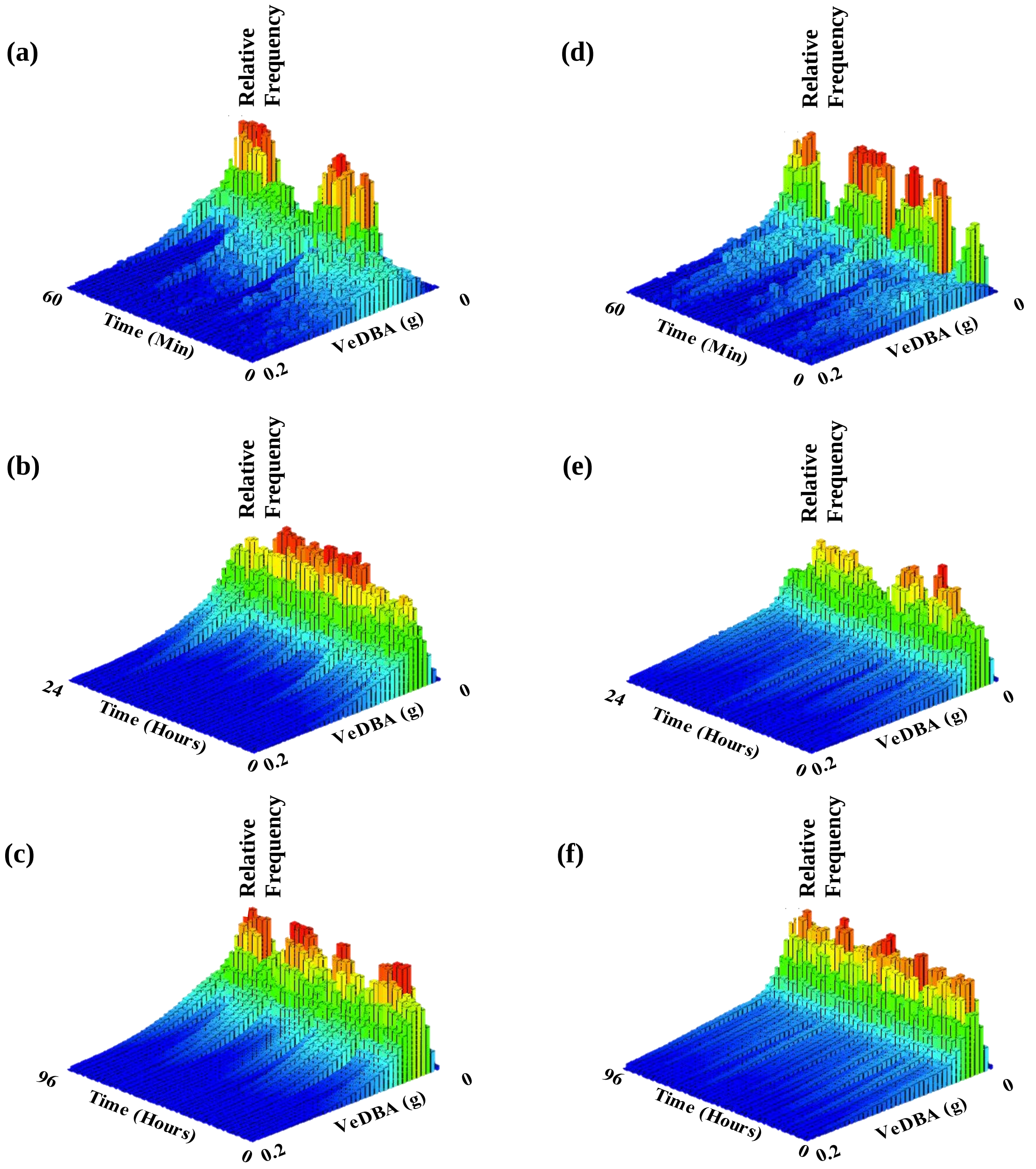

Figure 5. Histograms showing allocation of activity (VeDBA) over time, of two example turtles: T324, which was considered healthy (figures on the left; a, b and c) and T331 which had intestinal gas and buoyancy issues (figures on the right; c, d and f). Histograms cover time periods of one hour (a and d), 24 hours (b and e) and four days (c and f). Bar colour and height indicate the relative number of observations within the time interval. In both example turtles, lower VeDBA values occurred most frequently (red bars). Note that the individual with intestinal gas exhibited erratic periods of high VeDBA, showing high effort in bursts compared to the healthy individual which showed clear periods of rest and high VeDBA (swimming).

3.3 Pitch, Roll, and Directionality

G-sphere visualizations of body pitch and roll, (derived from the acceleration data, which showed the time allocated to different pitch and roll values, i.e., body attitude (Wilson et al. 2016) indicated slight differences between healthy and unhealthy rehabilitating turtles (Figure 6). Animals with serious illnesses and reduced activity generally occupied a smaller area of the g-sphere relative to healthy turtles; however, individuals recovering from gas emboli tended to occupy a slightly greater area. Magnetometry plots (m-plots, see Williams et al. (2017)) showed clearer differences in movement behaviour; unhealthy animals generally displayed greater variability in directionality than healthy ones (Figure 7). Variability in orientation was also observed in a turtle that underwent MRI, with rose plots indicating directionality becoming more concentrated with time post-scan (Figure 8).

4. Discussion

The purpose of this study was to investigate the effectiveness of animal-attached loggers to elucidate behaviour in order to assess animal health in sea turtles undergoing rehabilitation. Behaviour is recognized as having the potential to serve as an indicator of health (Abou-Ismail et al. 2007; Burman et al. 2007; Scollo et al. 2014; Guesgen & Bench 2017; Shorter et al. 2017), so movement-sensitive tags, such as the DDs used in this study, could be used to provide an objective and time-efficient way of quantifying behaviour *via* the creation of TDBBs for health. Our statistical analysis, although with limited power, indicated that behaviour (specifically the relationship between mean VeDBA and the number of 45º turns per hour) differed significantly between healthy individuals and those with external injuries (e.g., flipper damage, carapace trauma and skin lesions).

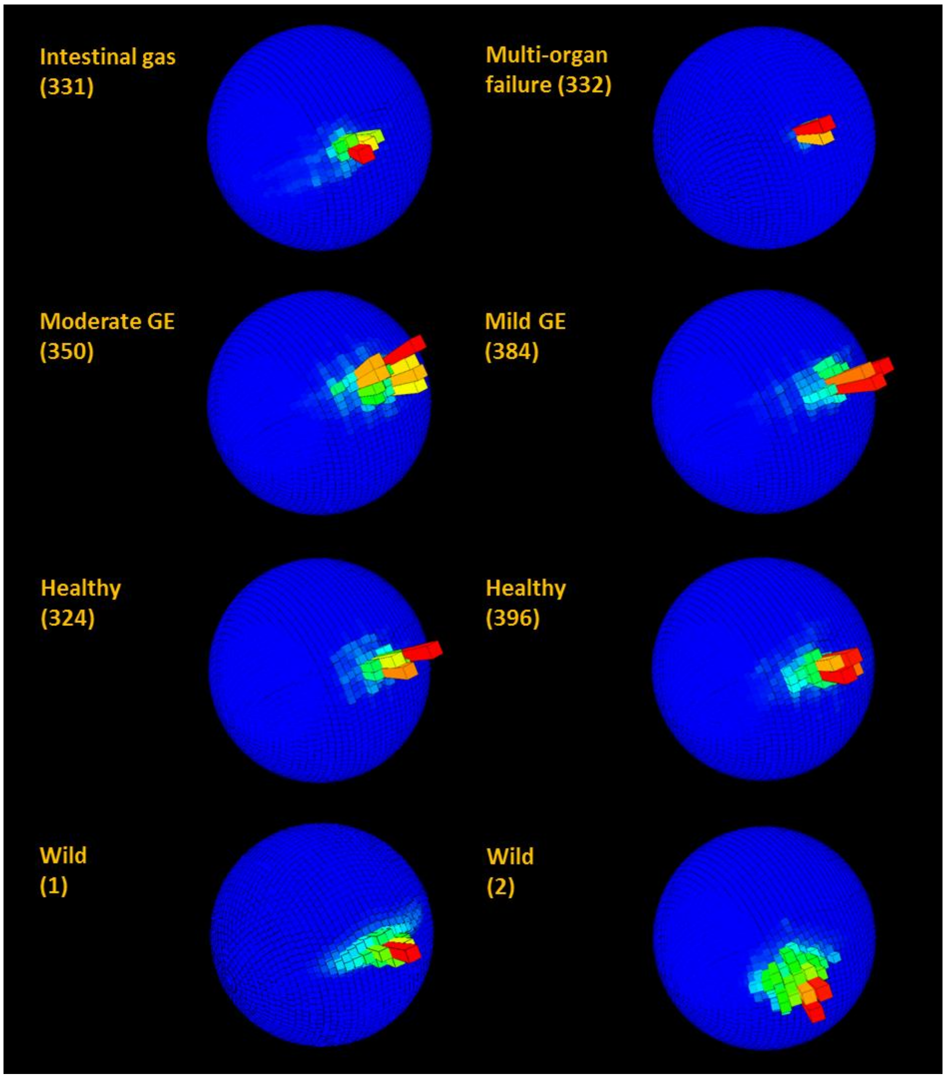

Figure 6. Spherical histograms showing relative time (bar height) over 24 hours allocated to body pitch and roll (see Wilson et al. (2016) for more detail) in rehabilitating and wild turtles. Individuals in rehabilitation are identified by number (see Table 1) and suffered from various diseases including gas emboli (GE). Despite the superficial semblance of plots, very infirm individuals (in particular T332) with reduced activity generally occupied a small area of the sphere relative to healthy and wild turtles, whereas individuals with mild to moderate GE generally occupied a slightly greater area. Note the overall line made by the placement of bars within the histogram in the wild individuals, which corresponds to increased pitch variation because the animals were diving in deeper water.

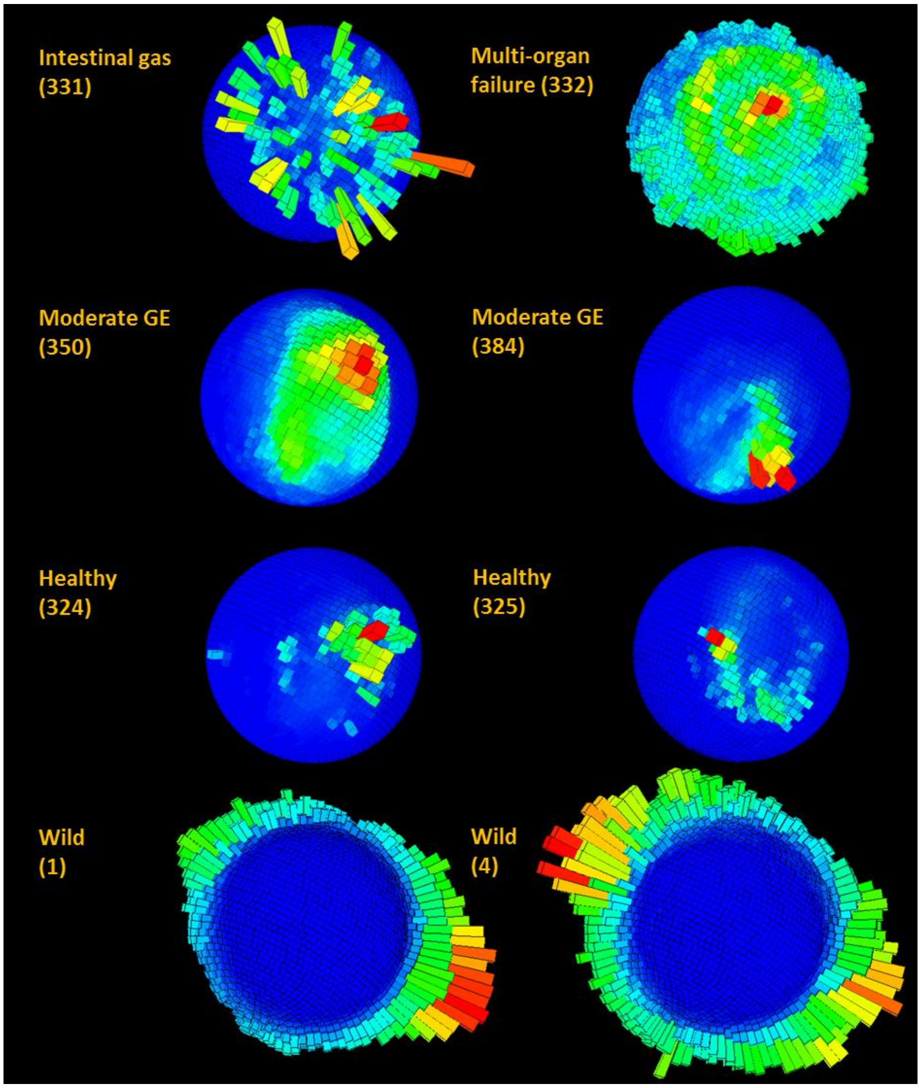

Figure 7. Spherical magnetometer histogram plots (m-plots see Williams et al. (2017)) showing time allocation to direction (indicated by the clarity of the central ring– an animal that spends equal time facing all directions will have a perfectly formed, equal height ring) with deviations from the circle indicating non-horizontal body angles in turtles under human care and two wild turtles over 24 hours according to condition. Note the clear ring in the wild animals and the high directionality in the captive individuals.

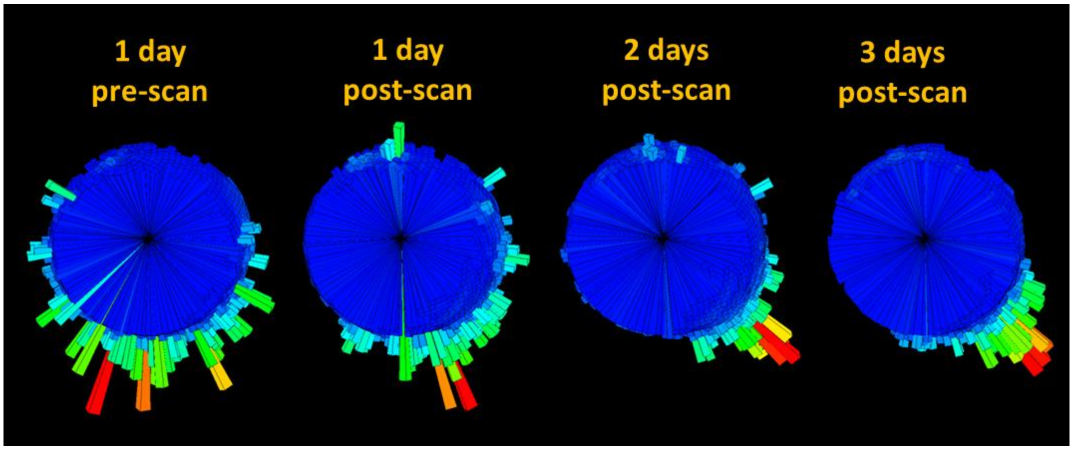

Figure 8. Body orientation histogram (rose plot) over 24 h time-periods for turtle T383 prior to undergoing an MRI scan and for the 3 days following this. Bar length denotes length of time allocated to each direction (the mode is shown in red). Note how the appreciable variability pre-MRI scan appears to diminish with time after the scan.

Although this study focused on loggerhead turtles undergoing rehabilitation following fisheries interaction, the approach could potentially be adopted for a suite of aquatic (Shorter et al. 2017), terrestrial (Mason & Rushen 2008) or aerial species (Shepard et al. 2008). Our limited access to animals precluded us from presenting exhaustive data analyses from a suite of turtles of defined size, unknown sex and in various states of health, so by and large we present sample data as examples of the features that can be resolved using this technology and speculate how these relate to health status.

4.1 Behaviour and condition

After being released into a holding tank, bycatch turtles generally exhibited a period of elevated activity ranging from half an hour to several hours (when examined over a 24-hour period). In part this was probably due to tagging occurring during the day when activity levels were higher and there was more disturbance (caused by feeding and tank cleaning). In healthy turtles, this initial increase in activity typically lasted less than two hours whereas in individuals with gas emboli this was always three hours or more. This disparity could reflect the condition of the turtle, especially given that individuals with gas emboli have been known to display abnormal behaviour, ranging from hyperactive to catatonic (García-Párraga et al. 2014). However, disparities may also arise from a variety of other factors: side-effects of hyperbaric treatment, stress induced by handling (Grandin 1997; Moberg 2000; Carere & Oers 2004; Waiblinger et al. 2004; Gourkow & Fraser 2006; Hemsworth et al. 2011), tag attachment (Bridger & Booth 2003; Geertsen et al. 2004; Vandenabeele et al. 2011; Walker et al. 2011; Thomson & Heithaus 2014), re-entering the water after many hours on land and being released into an unknown environment (Teixeira et al. 2007; Roe et al. 2010). These factors make it difficult to know what truly 'healthy' turtle behaviour in a rehabilitation centre looks like using tag data. Nonetheless, significant behavioural differences in relation to activity and turn rate were found between 'healthy' turtles and those with external injuries (see section 4.5). Our statistical analysis also indicated that within group values had a high similarity, thus indicating that once healthy, turtles in rehabilitation exhibited similar behaviour.

Interestingly, the relationship between activity level and turning for turtles with internal injuries did not differ significantly from healthy animals. However, the internal injuries included in analysis were unlikely to affect energy expenditure and movement to the same degree as missing part of a flipper or sustaining severe carapace trauma. Most of the turtles (six out of eight) that suffered internal injuries were admitted with gas emboli and as such were only released into a tank once they had no gas bubbles left in their blood (as per the standard veterinary procedure). By this time these individuals may have recovered sufficiently to exhibit activity levels and turning rates akin to those of 'healthy' turtles. Potential differences between healthy animals and those with internal damage may have also been more apparent if two turtles with severe internal complications (T331 and T332) could have been included in statistical analysis. They were excluded from the analysis because the available water mass in which they had to move was unknown and our analysis suggested that tank size significantly affected behaviour.

Further behavioural comparisons of healthy turtles and individuals recovering from internal injuries such as gas emboli and intestinal gas indicated other potential differences relating to condition. Rest and active periods (typically composed of active ascents and descents interspaced with resting on the tank floor) were often less defined in convalescent turtles; not only did rest intervals appear more sporadically, but acceleration traces were noisier, probably indicating impaired movement control during recovery and/or post hyperbaric treatment. Magnetometer plots also indicated a difference between healthy rehabilitating turtles and those with gas emboli, the latter tending to display less directionality, potentially indicating impaired stability or movement control. Differences between healthy and infirm individuals with intestinal gas (T331) and multi-organ failure (T332) were even more apparent, with deviations covering almost half, or more, of the m-sphere, respectively. Indeed, the trace that differed most from the others was that of turtle T332; the animal remained at the surface and was relatively inactive for the duration of tagging (four days). As with many animals, maintaining a very low energy state and fatigue can be indicative of serious illness and a precursor of death (Drake et al. 2003; Gailliot et al. 2006). With a sufficient sample size, a range of expected energy levels (including the duration of ‘rest’ and ‘active’ periods as well as changes in VeDBA over time) for a given condition could be calculated, although these would also have to take into account turtle age, size, sex and surroundings i.e., enclosure size, enrichment and water temperature, if found to be relevant.

4.2 Metrics that might indicate general activity patterns

We suggest that it should be possible to assess health status using VeDBA as a metric of general activity, for example, the comparison of animals with gas emboli *versus* healthy individuals, aside from showing different postural changes, also demonstrated different VeDBA signatures. The paddling behaviour in diseased animals was more intense and prolonged than in healthy individuals. This could have been a side effect of being out of the water for a number of hours and/or hyperbaric treatment, which is thought to increase activity (Vicente Marco *pers. comm.*). Increased activity was also observed in the individual with intestinal gas. The link between VeDBA and physical condition was clearer in this case because the extra gas within the body caused greater buoyancy, making it more difficult to dive and requiring more vigour (Minamikawa et al. 2000). Thus, while attempting to dive underwater in order to rest on the tank floor, as is normal, individuals with overall body densities less than that of seawater must spend additional energy paddling to overcome the added buoyancy, resulting in elevated VeDBA during descent (Wilson & McMahon 2006).

A very different VeDBA signature was observed for the individual that died of multi-organ failure; our study animal never reached the bottom of the tank to rest (*cf.* Minamikawa et al. 2000). Instead, periods of attempted descent were interspaced with periods of rest at the surface. This pattern became clear when comparing the VeDBA trace (which was consistently low) with that of depth.

4.3 Metrics that might indicate disease/injury

We suggest that diagnostics of health could be based on multiple parameters in a disease/injury identification key that could be combined to form specific TDBBs. Thus, an indication that a turtle has problems with buoyancy could be provided by having: (i) a higher incidence of body pitched down, (ii) a greater incidence of high VeDBA and (iii) greater amplitude in VeDBA cycles stemming from exhaustion (recovery time at the surface due to greater oxygen use while underwater). This, for example, was observed in an individual with intestinal gas which had higher buoyancy than controls and was unable to descend the water column and reach the bottom of the tank without excessive paddling. A clear signal that this was the case was given by body pitch angle since the animal spent a large proportion of the time swimming down (with the body pitched forward) against buoyancy, whereas control animals only had the body pitched forward for the short periods they spent moving from the water surface to their preferred depths.

In fact, the body attitude of the individual with intestinal gas not only differed with respect to that of the healthy animal with regard to pitch, for which a mechanistic basis can be proposed (see above), it also differed with respect to roll (as observed in magnetometer plots– *cf.* Williams et al. 2017), indicating apparent instability which was not the case in healthy animals. This apparent lack of control was also observed in example individuals recovering from gas emboli and with multi-organ failure. We suggest that consideration of body posture, particularly in sea turtles (and potentially other aquatic species), and derivatives of this, such as rate of change of body posture, would be a useful way of documenting deviations in health status from the ‘norm’.

Additionally, assessing changes in body posture before and after treatment could help to track animals through recovery and elucidate potential negative side effects of certain procedures, in particular, MRI scans, which expose animals to high magnetic fields in order to generate high quality diagnostic images (superior to those of radiographs and ultrasound) (Rübel et al. 1994; Walzer et al. 2003; Aryan et al. 2006; Thornton et al. 2005). Despite evidence that sea turtles rely on geomagnetic cues to navigate and reach specific nesting and feeding sites (Lohmann et al. 2004; Putman et al. 2011), MRIs have been widely used in anatomical examinations of the ear (Ketten & Bartol 2005), head (Arencibia et al. 2012) and coelomic structures (Valente et al. 2006), as well as to investigate internal injuries caused by the ingestion of debris (Gasau & Ninou 2000) and internal tumours in turtles with fibropapillomatosis (Croft et al. 2004). To date, no study has considered whether exposing turtles to intense magnetic fields could impair navigational abilities post-release. In this study, we presented information of the directionality in a single turtle (that had been admitted with gas emboli) pre- and post-MRI, which indicated increased directionality in the days following the scan. The implications of this possibly transient effect and whether this behavioural change should be attributed to recovering from gas emboli or magnetic field exposure or another factor is unknown and requires further study.

4.4 Monitoring periods

After initial release into rescue tanks, VeDBA values from afflicted turtles during day one of tagging were typically within one standard deviation of healthy turtles. However, the probability of values from infirm turtles falling outside of this range would be likely to increase as a function of time and treatment; for example, sedatives would reduce activity whereas hyperbaric treatment and physiotherapy may increase it. Certain afflictions were more likely to alter behaviour only in the short-term. For example, most turtles with gas emboli often did not exhibit defined active and rest periods (as observed in healthy turtles) for a few hours after release into a rescue tank. Nevertheless, veterinary diagnostics indicate that after hyperbaric treatment, turtles show full gas reabsorption. It is worth noting that in cases with severe gas emboli, bubble formation may have caused permanent damage. Observations also indicated that turtles were more active during daylight hours and therefore diel patterns should be taken into account when considering how long animals should be monitored. For many turtles, a second peak in VeDBA was observed some 20 hours post-tagging, between 8:00 am – 12:00 pm (noon), which was consistent with increasing light levels (the start of a new day) and tank cleaning and feeding (which takes place most mornings).

The infirm turtles that differed most from the general ‘healthy turtle’ trend were T342 and T347; both had suffered traumas to the carapace and the latter also had a partially amputated flipper. The two turtles were first tagged some months after arriving at the centre (T342 was tagged two months after arriving and T347 almost seven months) due to treatment and/or injuries making the standard tag deployment procedure not feasible. The VeDBA values exhibited by T342 were consistently below the mean of healthy turtles whereas for T347 they were within the healthy turtles’ range for the first 12 hours and then rose markedly above them. This rise, which peaked between 10:00 am – 12:00 pm, coincided with tank cleaning (which may cause animals some disturbance) and feeding. For T347, all swimming, but in particular descending to the bottom of the tank in order to eat, required exertion that was clearly greater than the norm, thus illustrating the potential for injury-specific feeding signatures as part of TDBBs relating to physical condition. The data from T342 and T347 also demonstrate that certain injuries, especially those involving flippers or carapace trauma, have long-lasting or even permanent effects on behaviour. Consequently, monitoring the activity of such individuals at regular intervals over the long-term could provide a valuable tool when assessing recovery, especially if specific TDBBs defining expected improvements existed and could be used in comparison.

In future, baseline data on expected VeDBA values for a variety of conditions through time could be determined by attaching DDs to turtles in rehabilitation centres and aquariums around the world. Such collaboration would be needed to build a behavioural repository of certified healthy animals, taking into account turtle size, sex, season, water temperature, enrichment and enclosure size/available water mass. Although we found no significant relationship between available water mass and VeDBA, our analysis included turtles in various states of health and was only based on data from the first 24 hours of tagging (whilst this should encompass diel changes, it would not take into account more longitudinal trends). The collection of such baseline data is of primary importance when defining suitable lengths of time to monitor rehabilitating animals.

4.5 Metrics that might indicate changing state and behavioural breadth

This work begins the examination of the health of managed care animals by comparing the behaviour of rehabilitating turtles with various diseases and injuries. The small sample size makes this necessarily speculative at the moment, but the results provided should encourage researchers to develop a common data base, or at least to share data, in order to gain the statistical power to differentiate conditions using tag-derived metrics confidently. In addition to increasing the sample size for turtles, it would benefit zoological institutions to expand the work to other taxa (*cf.* Shorter et al. 2017; Ropert-Coudert et al. 2009). It is also important for workers using DD-type tags (see Johnson and Tyack 2003) incorporating *inter alia* sophisticated and powerful sensors such as accelerometers and magnetometers, to recognize the large number of potentially important variables that can be gleaned from such devices to aid in the discrimination of differing behavioural states. These include, but are not limited to, animal heading (Williams et al. 2017), saccadic movement (Wilson et al. 2015b) and rates of change of a suite of parameters (e.g., depth, pitch, roll and yaw) over different time intervals (Wilson et al. 2018) and there is an increasing number of analytical systems available to help in this (e.g. Walker et al. 2015a; Wilson et al. 2018).

There are, however, some metrics that will be more universal than others, and an example of this is VeDBA– a powerful metric that codes for overall body activity and acts as a proxy for metabolic rate (Qasem et al. 2012). Normally, we would expect the healthiest animals to be the most active, although the particular cases of intestinal gas and gas emboli show that this is not always true. Another less frequently used but extremely useful derivative is that of animal heading (turning) (Bidder et al. 2015; Walker et al. 2015b; Williams et al. 2017). Unlike VeDBA, which is derived from acceleration data and as such is affected by currents in air and water that can distort the signal-to-noise ratio (Halsey et al. 2011b), compass heading is not. VeDBA is also of limited use when examining the behaviour of slow moving, relatively inactive or gliding animals that maintain a steady velocity for extended periods, for example turtles (Wyneken 1997; Eckert 2002) and soaring birds (Williams et al. 2015). In such cases, using magnetometers and examining movement patterns about the yaw axis may elucidate behaviours that are not evident in acceleration data alone (Williams et al. 2017). We found that VeDBA and heading in unison showed a promising way of differentiating between healthy and infirm turtles with external injuries. This was not surprising as severe flipper damage and carapace trauma affecting the spinal cord (as observed in individuals T342 and T347) had a clearly visible impact on the swimming and manoeuvrability of individuals. Critically though, it is specifically the combination of parameters (here dynamic acceleration and turning rates) that demonstrates that mixed sensor outputs can be particularly useful in TDBBs for state and our work is a first step in this direction. Other combinations, such as that of a body health index (*cf.* Clegg et al. 2015; Shorter et al. 2017; Schiffmann et al. 2018) with tag-derived movement metrics (like VeDBA and/or turning) may also reveal useful links between behaviour and health. Although tagging animals with obvious external injuries would be unnecessary for diagnostic purposes, examining their behaviour over time could be beneficial in order to track recovery and determine when behaviour has returned to 'normal' relative to healthy individuals. In some cases, behavioural biomarkers may indicate that an animal will never be fit for re-release into the wild.

4.6 Implications for other species

Given the ever-growing welfare concerns for animals maintained in zoos and aquariums (Johnson & Tyack 2003; Shepard et al. 2008; Ismail et al. 2012; Draper & Harris 2012; Feldman 2016) and the myriad research opportunities that these venues provide, it is surprising that little quantitative information (which is readily available *via* biologging) exists in relation to the activity and health of most species (Flint & Bonde 2017; Shorter et al. 2017). This is especially pertinent to managed marine vertebrates (particularly cetaceans and other pinnipeds), whose presence in aquariums is regularly scrutinised (Rose et al. 2017). As such, current health and welfare assessments and monitoring practices, which generally rely on qualitative observations (including what individuals eat and social interactions) could be greatly aided by the collection of behaviour in a quantifiable manner (Shorter et al. 2017). Studies using tags on farmed animals show how advantageous this could be; for example, improved lameness detection *via* leg-mounted accelerometers on dairy cows (Thorup et al. 2015).

In contrast to observational monitoring, which takes time and has a large degree of subjectivity (Broom & Johnson 1993; Rushen 2003; Lawrence 2008; Rose et al. 2017), biologging enables the collection of quantitative data in a fast (often at several Hertz) and unbiased manner (Block 2005; Sherub et al. 2017). Furthermore, information is recorded in sufficient detail to; (i) develop species-specific guidelines to standardise captive assessments, (ii) determine if adequate welfare requirements are being fulfilled, i.e., by defining what constitutes ‘typical’ or ‘healthy’ behaviour and (iii) provide guidance on whether an animal is suitable for release after rehabilitation (Rose et al. 2017). This has particularly important implications for a wide range of species (including fish, sea turtles, birds, pinnipeds and cetaceans) that are frequently injured in fishery related interactions or by marine debris (Raum-Suryan et al. 2009; Adimey et al. 2014; Gall & Thompson 2015; Jambeck et al. 2015; Nelms et al. 2015; Stelfox et al. 2016).

Unlike the animals in human care, logging devices have been widely used with their wild counterparts (Eckert 2002; Shorter et al. 2017). The information derived from these applications is highly valuable as understanding natural behaviour and ecology is key to informing appropriate welfare standards for animals in captivity (Eckert 2002; Shorter et al. 2017) and the wild (Rose et al. 2017). It also informs critical decisions such as whether to conserve natural habitats or recreate them artificially– these decisions usually involve vulnerable animals (for example dugongs and manatees) and can have major consequences (Rose et al. 2017).

4.7 Limitations and perspectives

This dataset provides a small first step in demonstrating the usefulness of tags for collecting information on animals in human care. However, studies with a greater sample size and covering longer tag attachment durations are necessary to give proper statistical credibility to these initial findings. Nonetheless, significant behavioural differences (related to VeDBA *versus* the number of turns per hour) were found between healthy controls and turtles with external injuries to the flippers and carapace, suggesting that even with limited data, the utility of this tool is justifiable. Furthermore, comparisons between healthy individuals and those with gas emboli, intestinal gas and multi-organ failure, in the form of spherical plots revealed appreciable differences in orientation during a 24-hour time window.

Although our categorisation of turtle health status relied on veterinary diagnostic techniques (including blood sampling, radiographs and ultrasounds), the goal of creating illness specific TDBBs would be to limit the use of these potentially invasive and stress inducing procedures. In addition, the use of tags that transmit data would enable remote data collection in real time (Laske et al. 2014; Wilmers et al. 2015), both reducing animal handling and speeding up diagnosis/ our ability to track an animal’s recovery. This would make our approach suitable to a variety of different applications in captive animal monitoring.

The financial and societal value of many species in managed care means that even limited data such as ours are appreciably better than nothing if it helps to enhance animal health and well-being. Indeed, within the zoo veterinary field, approaches are developed by slowly increasing findings from individual animals to larger numbers (Swaisgood & Shepherdson 2005; Kuhar 2006). Reaching the appropriate sample size required to obtain biologically or statistically significant results is a notable difficulty, often because few (if any) individuals are maintained in zoos/aquariums (Swaisgood & Shepherdson 2005; Kuhar 2006) and data sharing between organisations may not be possible for ethical and/or legal reasons (although data sharing platforms that encrypt data may provide a solution for collaborative research and data pooling in certain circumstances) (Wolfson et al. 2010; Doiron et al. 2012; Vuong et al. 2022). Furthermore, in this circumstance, animals were tagged opportunistically as they entered the rehabilitation centre with a variety of different injuries and diseases, which reduced suitable comparisons.

4.8 Future directions

Obvious further developments on the work presented here would be to equip more individuals with tags in order to augment sample size and validity and test the various metrics highlighted in this paper. After establishing TDBBs in loggerheads, the next step would be to trial them on other sea turtle species to gauge whether they were transferable or easily adaptable. Another line of work would be to ascertain whether TDBBs could be made specific to not just different diseases and injuries but also animal states (i.e., positive: happy or negative: sad, fearful, aggressive etc.) in order to use behaviour as a measure of welfare (Benn et al. 2019). If successful, TDBBs could be adapted to fit other bycaught species in the same way that farm animal welfare assessments have been modified for zoos (Fraser 2009; Hill & Broom 2009) and aquariums (for example the ‘C-Well’ welfare assessment index for dolphins in managed care (Clegg et al. 2015). In other words, TDBBs could be established for other species undergoing rehabilitation and release with more complex behavioural repertoires such as cetaceans and pinnipeds. Furthermore, motion-sensitive data from animals in human care and wild conspecifics could be compared in order to define a set of expected behavioural states and/or activity levels for numerous species housed in zoos/aquariums to help ensure their welfare. Finally, animal health is an increasing concern for wild populations, and appropriate validation of objective TDBBs in managed care populations could be of relevance when studying health and welfare in free-ranging animals.

5. Conclusion

This manuscript showcases how data collected from motion- and orientation-sensitive animal-attached technology can be used to derive metrics which may aid animal health assessments and that could in time be combined to form an injury/disease identification guide. For example, data visualization showed behavioural differences between ‘healthy’ sea turtles and individuals suffering gas emboli and intestinal gas, with the latter apparently paddling more frequently and spending more time with the body pitched downwards (presumably in order to compensate for increased buoyancy). Appropriate visualisation showed such diagnostic patterns immediately without complex data analysis. We also found that VeDBA and turning (compass heading) in unison showed a promising way of differentiating between healthy and infirm turtles with external injuries to the flippers and carapace. Given this, we propose that the use of motion-sensitive tags could aid diagnosis and inform therapy, in particular cases follow-up, monitoring improvement and response to treatment. This is particularly relevant to turtles, given the numerous rehabilitation programs for bycatch sea turtles in operation. We suggest that establishing tag-derived behavioural biomarkers (TDBBs) for health in these animals based on the visualisations and metrics discussed in this paper is therefore timely and should both facilitate and improve the rehabilitation process.

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Chapter 3

Photography by Alejandro Usategui

Health monitoring in captivity *via* tags: do turtles recovering from ‘the bends’ behave differently to ‘healthy’ turtles?

Abstract

Remote health monitoring devices, although in their infancy, could form powerful health assessment aids, elucidating specific animal movement behaviours indicative of health or a given disease. Decompression sickness is a condition caused by dissolved gases in the blood coming out of solution and forming gas emboli (GE) within the vessels, tissues, and organs of the body after a rapid pressure decrease (i.e., during the ascent of a dive). In recent decades GE have been reported in a variety of breath-hold diving vertebrates, including sea turtles, following anthropogenic disturbances. This study used motion- and orientation-sensitive tags to record the behaviour of bycaught loggerhead turtles in rehabilitation with varying degrees of GE; devices were also fitted to healthy turtles at the rehabilitation centre for comparison. Key aspects of aquatic animal movement behaviour, including surfacing, activity level, attitude consistency/stability and angular movement were investigated. These metrics could be readily derived from tag data and focused on behaviours that were expected to vary in accordance with health status, making them ideal indicators of condition.

I focused my analysis on the movement metrics that differed most between the groups as these had the best potential of forming useful indicators of health or tag-derived behavioural biomarkers (TDBBs). The variance in body attitude (i.e., pitch and roll values), the number of 45° turns and the mean angular velocity per hour showed most promise when differentiating between healthy and recovering turtles. The results of this work demonstrate the promising potential of tag-derived metrics for the systematic and remote health monitoring of turtles and other rehabilitating animals, increasing our knowledge of behavioural biomarkers and facilitating the work of veterinary staff.

1. Introduction

Decompression sickness (DCS; also referred to as the bends) describes a condition resulting from dissolved gases coming out of solution and forming gas bubbles within the body upon depressurization (Francis & Gorman 1993; Francis & Mitchell 2002; Vann et al. 2011). DCS may refer to complications arising from underwater diving decompression (i.e., during ascent) as well as aerial depressurization events during changes in altitude (Egi & Brubakk 1995; Bosco et al. 2018). Although bubbles may technically form of any gas, nitrogen bubbles are the most common when atmospheric air is breathed before diving because nitrogen is the most abundant gas and is not metabolized in the body (Francis & Gorman 1993; Doolette & Mitchell 2001; Bosco et al. 2018). Upon diving, the partial pressure of nitrogen in the lungs increases resulting in the absorption of N_2 into the tissues and with extended time, the tissues become saturated (Francis & Gorman 1993; Doolette & Mitchell 2001; Francis & Mitchell 2002). If the pressure decreases rapidly (during ascent), the nitrogen within the tissues bubbles out, forming gas emboli within the blood vessels, tissues and organs of the body (Doolette & Mitchell 2001; Francis & Mitchell 2002). DCS has most often been reported in human divers, with symptoms ranging from headaches, joint pain, rashes and in more extreme cases, paralysis and death (Francis & Mitchell 2002; Vann et al. 2011). DCS related symptoms are caused by bubble formation or gas emboli (GE) and may appear within half an hour to several hours post depressurization (Francis & Mitchell 2002; Vann et al. 2011).

There are two main factors contributing to the likelihood of developing DCS. First, is the duration and rate of gas absorption at an increased pressure, i.e. on longer and deeper dives, more gas is absorbed into the body tissues (Henry's Law) and second is the duration and rate of outgassing upon depressurization (i.e. shorter time intervals between dives and fast ascent rates allow less time for the absorbed gas to be dissolved/offloaded in the lungs, resulting in gases coming out of solution and forming bubbles in the blood and tissues) (Doolette & Mitchell 2001; Vann et al. 2011; Bosco et al. 2018).

Over recent decades, DCS-related symptoms have also been reported in a variety of breath-hold diving vertebrates following anthropogenic disturbances which may induce unusually rapid ascents; incidents have been linked to naval sonar, gear entanglement and bycatch with affected species including marine mammals (cetaceans and pinnipeds (Jepson et al. 2003; Jepson et al. 2005; Bernaldo de Quiros et al. 2012; Fernández et al. 2017)) and sea turtles (García-Párraga et al. 2014; Fahlman 2017; Portugues et al. 2018). It was believed that these animals do not normally suffer from pressure-related issues (such as GE and DCS) and such symptoms have not been recorded during natural dives ((Scholander 1940; Kooyman 1973; Lemaitre et al. 2009) and references therein). This is thought to be due to a suite of physiological, anatomical and behavioural adaptations that work in combination to circumvent many pressure-induced problems (Lemaitre et al. 2009). Normally, certain traits work to alter gas exchange in order to avoid excessive N_2 accumulation in the blood and tissues, allowing these animals to hunt and navigate underwater efficiently (Fahlman & Kayar 2003; Fahlman et al. 2007; Fahlman et al. 2009; Lemaitre et al. 2009). For example, diving vertebrates have been found to retain a limited amount of N_2 in their lungs or minimize N_2 uptake during each dive by way of pulmonary shunting, lung collapse and dive response (Fahlman & Kayar 2003; Fahlman et al. 2007; Fahlman et al. 2009).

It has been suggested that cases of DCS-related symptoms in diving marine vertebrates occur when external stressors disrupt the optimal functioning of these adaptations. For example, numerous mass strandings of cetaceans have occurred in close proximity to, and shortly after, the use of high-powered acoustic sources (e.g., naval sonar) with reports of DCS-like lesions observed during necropsies (Jepson et al. 2003; Fernández et al. 2005; Bernaldo de Quiros et al. 2012). Theoretical models have indicated that both physiological changes (e.g., increased blood flow resulting from stress and elevated CO_2) and behavioural alterations (e.g. increased dive duration and ascent rate) following exposure to sonar could lead to increased blood and tissue N_2 tension and consequently the risk of DCS (Fahlman et al. 2009; Bernaldo de Quiros et al. 2012; Fahlman et al. 2014).

In 2014, a study by García-Párraga et al. reported the presence of GE in bycaught loggerhead turtles, *Caretta caretta*; this was the first time GE was reported in any sea turtle species. Diagnostic imaging (radiographs, computed tomography and ultrasounds) revealed gas bubbles and their distribution within blood vessels, tissues and vital organs consistent with DCS (García-Párraga et al. 2014). It was also observed that afflicted animals displayed anomalous behaviour, ranging from being comatose to hyperactive (García-Párraga et al. 2014). The same study found that two individuals with DCS responded well to recompression therapy (in much the same way as humans experiencing DCS (Vann et al. 2011)) in a custom-built hyperbaric chamber with pure O_2 administered from a pressurized medical O_2 cylinder. Under increased pressure (within a hyperbaric oxygen chamber) gas bubbles in the blood stream are forced back into solution allowing them to be cleared gradually from the body over a period of hours (Francis & Mitchell 2002). Following treatment, turtles can recover fully unless gas bubble formation has caused lasting damage, for example, by rupturing a vessel or starving part of the brain from oxygen for too long (García-Párraga et al. 2014).

During recovery, changes in health status are likely to be reflected behaviourally because behaviour is manifest by specific movement and body attitudes (Wilson et al. 2008; Guesgen & Bench 2017; Shorter et al. 2017; Arkwright et al. 2020) and behaviour can indicate condition (Broom & Johnson 1993; Rushen 2003; Boissy et al. 2007; Lawrence 2008; Nathan et al. 2008; Scollo et al. 2014; Guesgen & Bench 2017; Benn et al. 2019)). Therefore, the development of multi-sensor animal-attached tags, recording movement parameters such as body acceleration and angular velocity at high frequency, has potential for enabling the delineation of condition-specific behavioural traits (Shepard et al. 2008b; Wilson et al. 2008; Ropert-Coudert et al. 2009; Wilson et al. 2016; Shorter et al. 2017; Lennox et al. 2018; Arkwright et al. 2020; Gunner et al. 2020). If behavioural traits that can be quantified by sensors, can in turn reliably assess the condition, i.e., health status of an animal, sensor technology may offer a novel potential for the systematic monitoring of animal health (Thorup et al. 2015). Movement-based metrics that can be linked to health condition, could be used as tag-derived behavioural biomarkers (TDBBs), aiding in the systematic assessment of an individual's recovery and remote monitoring of health status.

Motion- and orientation-sensitive tags were used to record the behaviour of rehabilitating bycatch loggerheads. Turtles undergoing rehabilitation at the 'Arca del Mar' rehabilitation centre (located within the Oceanogràfic aquarium, Valencia, Spain), were often admitted with bycatch-related external and/or internal injuries, including GE and decompression sickness (García-Párraga et al. 2014; Fahlman et al. 2017). The overarching aim of this study was to examine the extent to which the movement behaviour of 'healthy' turtles differed from that of turtles recovering from GE, as determined *via* multi-sensor animal-attached tags. My analysis concentrated on movement metrics that differed most between the groups, as those metrics had the best potential of forming TDBBs. A series of hypotheses were established, based on four key aspects of aquatic animal movement behaviour that were expected to vary with turtle health status:

1. *Surfacing behaviour*. Healthy turtles maintained in the rescue centre tanks typically appear to rest on the tank floor and ascend to breathe only every 10–20 minutes whereas turtles recovering from GE tend to lack the clear rest/bottom periods and generally surface more regularly.

2. *Activity measured via acceleration metrics*. If healthy turtles spend more time on the tank floor at rest and only momentarily ascend to the surface to breathe, they should exhibit movement profiles with longer periods of little to no movement interspersed with short bursts of faster movement. If recovering turtles spend less time at rest, they should have more consistent, i.e., less interrupted, movement trajectories.

3. *Attitude consistency/stability.* GE related injuries may impair manoeuvrability and lead to instability, resulting in greater variation in body attitude (pitch and roll) in recovering turtles than healthy ones (Arkwright et al. 2020).

4. *The extent of angular movement*. Turtles recovering from GE appear to rest less than healthy animals so that, other things being equal, they are more likely to exhibit higher numbers of turns per unit time.

2. Method

2.1 Study animals

The rehabilitating loggerhead turtles used in this study (see Table 1 for details), were all bycaught in small scale, gillnet, and trawling fisheries off the Valencian coast in the Balearic Sea, Spain. Fishermen, working in partnership with the Oceanogràfic Aquarium in Valencia, informed the veterinary staff who collected and transferred the bycaught animals back to the ‘Arca del Mar’

Table 1. Summary of tagged turtles including turtle identification number, bycatch origin, turtle weight (kg), curved carapace length (CCL), curved carapace width (CCW), cause of injury/disease (when known), tank size (L) and the turtle's state of health upon entry and on the date of tagging (following veterinary examination). Table ordered by turtle entry date (entry to and release dates from the rehabilitation centre, as well as the date of tagging, are provided in Appendix B). NB: gas emboli (GE) was categorised as mild, moderate, or severe; turtles that entered with GE were considered 'convalescent' when tagged within a couple of days of admission as they were only released into holding tanks following hyperbaric chamber treatment and once there was no sign of GE in the blood.

Turtle ID	Origin	Weight (kg)	CCL (cm)	CCW (cm)	Cause of injury/ disease	Tank size (L)	State of health upon entry	State of health when tagged
T344	Vinaroz	12.1	46.6	42.4	Trammel net	6000	Healthy	Healthy
T345	Vinaroz	17.1	54	49.1	Trammel net	3500	Healthy	Healthy
T350	Peniscola	15	50	45	Trawl/ bottom fishing	6000	Moderate GE	Convalescent
T359	Benicarlo	20.8	52	50	Trawl/ bottom fishing	6000	Moderate GE	Convalescent
T362	Cullera	13	46	42	Trawl/ bottom fishing	3500	Moderate GE	Healthy
T383	Cullera	11.6	44	40	Trawl/ bottom fishing	3500	Moderate GE	Convalescent
T384	El Saler	15.2	50	44	Trawl/ bottom fishing	1500	Mild GE	Convalescent
T385	Valencia	8.6	40.7	38.6	Trawl/ bottom fishing	3500	Healthy	Healthy
T393	El Saler	28.71	60	56	Trawl/ bottom fishing	6000	Moderate GE	Convalescent
T396	Vinaroz	22	59	49	Trawl/ bottom fishing	6000	Healthy	Healthy
T397	Gandia	7.3	39	35	Trammel net	3500	Drowned and was resuscitated	Healthy
T399	Cullera	5.7	40	35	Trammel net	3500	Healthy	Healthy
T402	Burriana	5.7	36	33	Trawl/ bottom fishing	1500	Healthy	Healthy
T403	El Perello	7.24	38	35	Unknown (found floating at surface)	3000	Healthy	Healthy

Turtle ID	Origin	Weight (kg)	CCL (cm)	CCW (cm)	Cause of injury/ disease	Tank size (L)	State of health upon entry	State of health when tagged
T404	Almenara	3.24	30	28	Unknown (found floating at surface)	3000	Wounded neck	Healthy
T405	Peniscola	34.24	64	59	Trawl/ bottom fishing	19000	Very mild GE	Healthy
T443	Vinaroz	10.77	43	40.5	Trawl/ bottom fishing	3000	Severe GE	Convalescent
T234	Burriana	85.5	83	77	Trawl/ bottom fishing	6000	Mild GE and fishing hook ingestion	Healthy
T449	Peniscola	10.41	45	38	Trawl/ bottom fishing	1500	Moderate GE	Convalescent
T452	Vinaroz	3.95	31	29	Trawl/ bottom fishing	3500	Healthy	Healthy
T458	Peniscola	41.28	60	60	Trawl/ bottom fishing	7000	Severe GE	Convalescent (died of septicaemia and intestinal issues of unknown cause)
T459	Burriana	12.15	45	40	Trawl/ bottom fishing	3500	Healthy	Healthy
T462	Benicarlo	13.47	45	40	Trawl/ bottom fishing	1500	Mild GE	Convalescent
T463	Vinaroz	7.5	40	36	Trawl/ bottom fishing	3500	Healthy	Healthy
T476	Vinaroz	15	46	47	Trawl/ bottom fishing	3500	Healthy	Healthy
T477	Gandia	9.9	41	40	Trammel net	3500	Superficial injury to the cloaca	Healthy
T481	Cullera	25.18	64	50	Trawl/ bottom fishing	3500	Healthy	Healthy
T482	Peniscola	30	56	56	Trawl/ bottom fishing	3500	Moderate GE	Healthy
T484	Peniscola	13.53	44	43	Trawl/ bottom fishing	3500	Mild GE	Healthy

Continued.

rehabilitation centre within the aquarium for examination. The duration between incidental capture and treatment upon arrival at the rehabilitation centre was unknown. Sea turtles were typically admitted with a variety of bycatch-related external and/or internal injuries including GE and decompression sickness (García-Párraga et al. 2014; Fahlman et al. 2017).

2.2 Rehabilitation

Upon arrival at the ‘Arca del Mar’, all sea turtles underwent a comprehensive health assessment including a physical examination, blood sample analysis and imaging studies (when required). The centre, which is managed by the Fundación Oceanogràfic in Valencia, Spain, has a permit from the Valencian Regional Government for sea turtle rehabilitation (including bycaught and stranded animals) and *post-mortem* examination. Turtle entry number (a running count of the number of turtles which enter yearly) was used as turtle identification; for ease, entry number (preceded with a ‘T’) was used to identify turtles within this manuscript (see Table 1). At the centre, rehabilitating turtles were housed in cylindrical tanks ranging 2–6 m in diameter with a water depth of 0.95 m; when there was not enough room to house turtles individually a central barrier was placed into tanks, dividing them in two. This resulted in tanks with differing available water masses of 1,500 L, 3,000–3,500 L, 6,000–7,000 L, and 19,000 L. All animals were maintained at the facility until their blood samples and behaviour had normalized and they were considered (by veterinary staff) to have regained a state of health fit for release.

2.3 Gas emboli and treatment

The presence of intravascular gas bubbles, whether in the blood stream, tissues or vital organs of bycaught loggerheads was established *via* diagnostic imaging studies (e.g., radiography, computed tomography, and ultrasound). The total amount and distribution of GE present was scored according to methods described in García-Párraga et al. (2014) and was as follows; (i) mild embolism: a small quantity of gas, visible only in the kidney area, (ii) moderate embolism: a larger amount of gas observed in the kidney area, minor vessels around the coelom and/or the liver full of gas and the occasional isolated gas bubble in the lumen of major vessels and heart chambers, (iii) severe embolism: larger quantities of gas present in the kidney, liver, major vessels and heart chambers. Individuals with moderate and severe GE (Table 1) received recompression treatment with pure O_2 from a medical O_2 cylinder (pressurized to ~1.5 Bar administered *via* a custom-built hyperbaric chamber (41cm x 77cm, internal height and diameter). For further details regarding the treatment and diagnosis process see García-Párraga et al. (2014). Turtles too large to fit into the recompression chamber (e.g. T458 in this study) received the pure O_2 from a medical O_2 cylinder whilst being maintained in a covered plastic tub with a few centimetres of water in the bottom.

Following recompression therapy, an ultrasound and a blood sample were taken in order to determine whether GE remained within any organs or the blood. Animals were only released into rescue centre tanks when no gas bubbles remained; in most cases this was the morning following hyperbaric treatment, although the gas sometimes took longer to clear for turtles too large to fit into the recompression chamber. Recompression therapy was typically conducted overnight, due to turtles usually being admitted in the afternoon/evening and continued during the day when necessary. Upon release into a rescue centre tank, individuals were considered to be in recovery (convalescent) and were monitored until their swimming, eating and blood values indicated that they had recovered.

2.4 Tagging

All turtles included in this study were tagged between November 2017 and April 2019. Animals were equipped with Daily Diary loggers (DDs, http://www.wildbytetechnologies.com/tags.html), motion- and orientation-sensitive tags, in order to record their behaviour and activity during rehabilitation. The devices had dimensions of 60 x 40 x 19 mm (± 10 x 10 x 6 mm), with masses ranging from 25–40 g, and recorded tri-axial acceleration, tri-axial magnetic field intensity, temperature and pressure at 20 Hz per channel (Wilson et al. 2008). Both acceleration (measurement range; ± 16 *g*) and magnetometry (recorded in Gauss (G) at 0.73 mG resolution, range; ± 0.88 G) were recorded along three orthogonal axes: dorso-ventral, lateral and longitudinal.

The DDs were glued to the second central scute of turtles' carapaces using a two-part epoxy (Veneziani Subcoat S, https://www.venezianiyachting.com/en/products/fillers), pre-mixed with water (Figure 1). During tag attachment, turtles were placed onto a foam mat within a plastic box and left for 10–20 minutes whilst the epoxy set. When feasible, animals were tagged shortly after admission and prior to being released into a rescue centre tank. Turtles that were healthy or that only had minor injuries were usually released into a tank some hours after arrival (following the results of the veterinary health assessment). Individuals that required treatment, such as those with GE, were generally released into a tank one or two days after arrival.

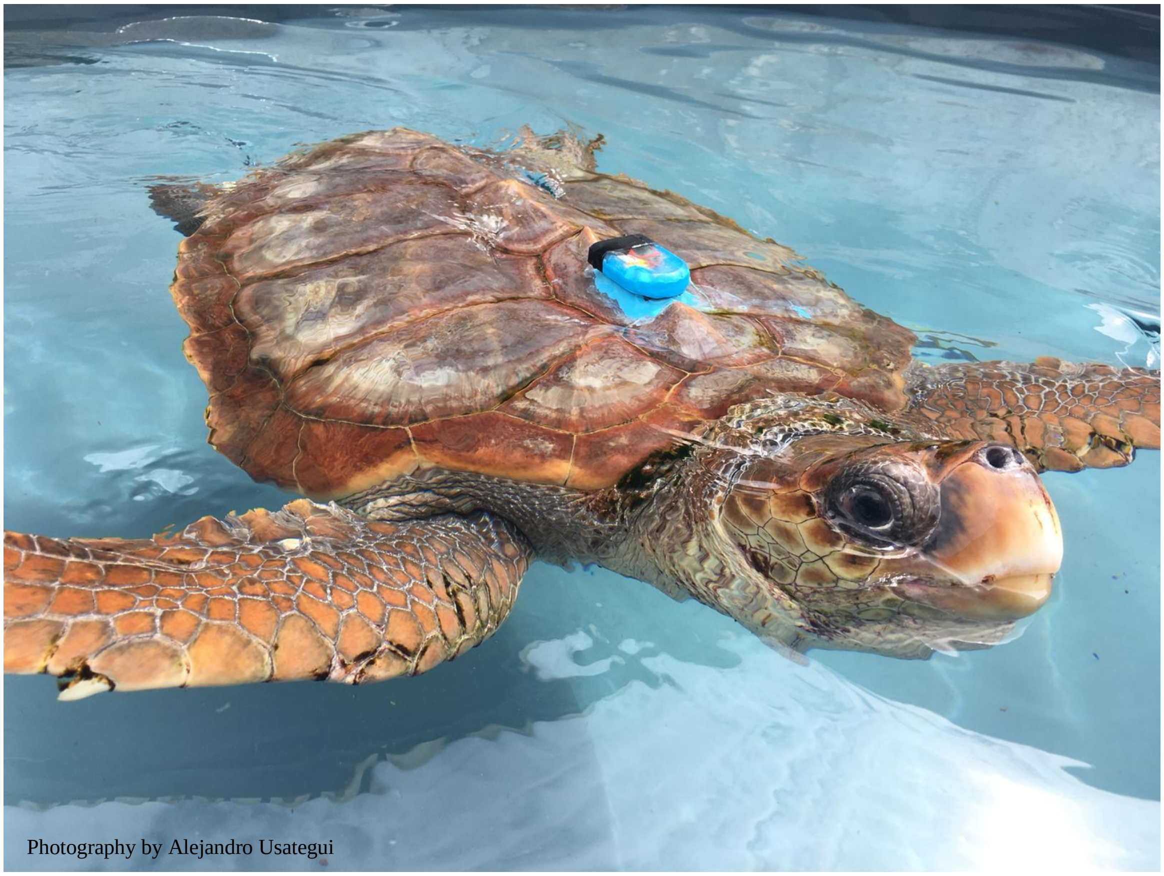

Photography by Alejandro Usategui

Figure 1. Loggerhead turtle with a Daily Diary tag (DD) attached to the second central scute of its carapace using a two-part epoxy.

2.5 Ethical statement

All animal treatment met with institutional guidelines and no medical procedures were carried out for this study. All research was approved by the Oceanogràfic Animal Care & Welfare Committee

(OCE-16-18) and the Swansea University, Animal Welfare Ethical Review Body (STU_BIOL_82015_011117151527_1).

2.6 Data analysis

Tag data were visualized using custom-designed software ‘Daily Diary Multi Trace’ (DDMT; http://wildbytetechnologies.com/software.html). DDMT software displays *inter alia* sensor lines of tri-axial accelerometry, tri-axial magnetometry, pressure and temperature on the y-axis against time on the x-axis. Useful derivatives for energy expenditure such as the vector of the dynamic body acceleration (VeDBA– see section 2.6.1.1) (Qasem et al. 2012) are also displayed along with options to calculate differentials of time sequential data and to run smoothing windows through the various channels.

2.6.1 Derivation of movement metrics

Metrics for defining movement behaviours for the four hypotheses stated above included: (1) pressure, (2) VeDBA (Qasem et al. 2012), (3) pitch and roll angles and (4) animal compass heading (i.e., orientation about the yaw axis in respect to Magnetic North) and angular velocity (see derivations below). Each of these was smoothed over two seconds to reduce noise and then undersampled from 20 Hz to 1 Hz for further analysis in RStudio.

2.6.1.1 Derivation of components of acceleration

The ‘static’ component of acceleration, i.e., the component of acceleration due to the pull of gravity, (which amounts to 1 *g* or 9.81 ms^{-2}) was computed by passing a moving average of a given window size (w) through a given sample (S_i) of each orthogonal channel’s acceleration (Fang et al. 2005). A two second window was applied in this study following Shepard et al. (2008a). The ‘static’ component is necessary for pitch and roll calculations used in the derivation of compass heading (see section 2.6.1.3) when the sensor is not level, as is generally the case following tag attachment (Bidder et al. 2015).

$$S_i = \frac{1}{w} \sum_{j=i-\frac{w}{2}}^{i+\frac{w}{2}} S_j$$

i is for the first index, *j* for the second.

The ‘dynamic’ component of acceleration was calculated by subtracting the ‘static’ acceleration of each axis from the raw acceleration (Bidder et al. 2015). Next VeDBA (*g*) was calculated by taking the sum of the dynamic acceleration (DA) values squared, from each orthogonal axis x, y and z (Qasem et al. 2012).

$$VeDBA = \sqrt{DA_x^2 + DA_y^2 + DA_z^2}$$

The VeDBA values obtained from this are instantaneous measurements of dynamic acceleration for a given sample.

2.6.1.2 Derivation of pitch and roll

Pitch and roll (°/s) were calculated using the static components of acceleration of the x, y, and z channels of the accelerometer, denoted with S_x, S_y and S_z and corresponding to the heave, surge and sway axes respectively (Bidder et al. 2015). Note: *atan2* is a function that calculates the angle between the two coordinates given as arguments (separated by a comma) and is available in Microsoft Excel as well as Matlab (Bidder et al. 2015).

$$Pitch = \left(atan2\left(S_x, \sqrt{S_y \bullet S_y + S_z \bullet S_z}\right)\right) \bullet \frac{180}{\pi}$$

$$Roll = \left(atan2\left(S_y, \sqrt{S_x \bullet S_x + S_z \bullet S_z}\right)\right) \bullet \frac{180}{\pi}$$

$$atan2(y, x) = 2\, arctan \frac{y}{\sqrt{x^2 + y^2}\ +\ x}$$

2.6.1.3 Derivation of animal compass heading

Animal compass heading (°) was calculated on a scale of 0–360° with a heading of 0° or 360° equating to the Magnetic North, 90° to the East, 180° to the South and 270° to the West (Gunner et al. 2020). DDMT software used calibration data, obtained by rotating the tag so that all orientations of roll, pitch, and yaw are covered (Williams et al. 2017). The data from the calibration forms a sphere when plotted on a tri-axial magnetic field intensity scatterplot, thus providing a reference frame of the vectorial sum of magnetometry data across the three axes (Williams et al. 2017). Using this, both ‘hard’ and ‘soft-iron’ distortions to the local magnetic field can be compensated (Gunner et al. 2020); hard iron deposits shift the position of the magnetic field causing the sphere to move away from its origin whereas soft iron deposits deform the magnetic field about the tag, resulting in the sphere becoming ellipsoid in shape (Gebre-Egziabher et al. 2006; Ozyagcilar 2012). Spherical fields were returned to their true origins and deformations of shape were corrected using an ellipsoid-fitting algorithm and correction factor (Bidder et al. 2015; Walker et al. 2015).

Angular rotation across pitch and roll axes (which are derived from the static acceleration), was used in the tilt correction procedure on each orthogonal magnetometer channel (Bidder et al. 2015). Compass data were normalised before each orthogonal channel was rotated according to pitch and roll. This ensured that the magnetometry channels were compensated, accounting for changes in angle resulting from postural offsets, with values corrected to give a horizontal co-ordinate frame (Bidder et al. 2015).

Compass heading (*H*) with respect to Magnetic North may then be computed according to:

$$H = mod\left(360 + \left(atan2(-m_y, m_x) \bullet \frac{180}{\pi}\right), 360\right)$$

where *mod* is the modulo operator and m_y,m_x are the normalized, ellipse fitted and co-ordinate frame-adjusted *x* and *y* channels of the magnetometer respectively (Bidder et al. 2015; Gunner et al. 2020).

Heading was then converted from degrees to Cartesian coordinates to deal with issues caused by yaw data being circular, (i.e., both 0° and 360° define the same point) and calculating the arithmetic mean (Pewsey et al. 2013). The arithmetic mean of individual angles ($\hat{\theta}$) was then calculated from sample trigonometric moments and the resultant units restored back to degrees ($\widehat{H}$).

$$\hat{\theta} = atan2\left(\frac{1}{n}\sum_{j=i}^{n} sin\left(H_j \bullet \frac{\pi}{180}\right), \frac{1}{n}\sum_{j=i}^{n} cos\left(H_j \bullet \frac{\pi}{180}\right)\right)$$

$$\widehat{H} = mod\left(360 + \left(\hat{\theta} \bullet \frac{180}{\pi}\right), 360\right)$$

For further detail regarding the steps and equations involved in the calculation of pitch, roll and compass heading see Walker et al. (2015), Bidder et al. (2015) and Gunner et al. (2020).

2.6.1.4 Derivation of absolute angular velocity

The absolute angular velocity, (AAV; °/s), movement metric was derived from the integration of pitch, roll and yaw axes absolute instantaneous angular velocity (Gunner et al. 2020). The differential angular velocity about the yaw, pitch and roll axes was denoted: *DAVY*, *DAVP* and *DAVR* respectively; where *x* is the *ith* value of yaw/pitch/roll (Gunner et al. 2020). The differential channels were calculated in DDMT after running a two second smoothing window through the values of each axis, using a stepping range of one second.

$DAVY = x_{j+1} - x_j$

$DAVP = x_{j+1} - x_j$

$DAVR = x_{j+1} - x_j$

$$AAV = \sqrt{(DAVY^2 + DAVP^2 + DAVR^2)}$$

Given that heading is circular and with no *bona fide* zero, designated high and low values were arbitrary. A logical expression for the *DAVY* prevented the rate of change surpassing 180°/s; the expression added 360 to values below -180 and subtracted 360 from values above 180 (Gunner et al. 2020). This remains biologically sound if angular velocity is calculated over a limited period as a change in compass heading from say 20° to 355°, is more likely to be the result of an animal turning 25° anticlockwise, as opposed to 335° clockwise (Gunner et al. 2020). The movement capabilities and speed of the study animal need to be taken into account when setting the sampling interval of *DAVY*. In theory the interval should be less than the time the animal in question would take to complete a 180° turn so as to avert errors when calculating rate change (Gunner et al. 2020). Thus, the greatest achievable angle for any given axis per second was 180°. The *DAVY* was also used to identify each time an animal rotated 45°, 90°, and 180° and whether the rotation was towards the right or the left. Both turn extent and direction were classified *via* conditional running cumulative sum functions in RStudio which reset to the starting orientation each time the condition, i.e., the specified angle threshold, was met.

2.6.2 Analysis of metrics used in hypotheses

2.6.2.1 Statistical analysis

Statistical analysis was performed, and figures were generated using RStudio (version 3.6.0, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/). The R packages used were: ‘ggplot2’ (Wickham 2016), ‘stats’ (version 3.6.2, (Pinheiro & Bates 2020)), ‘broom’ (version 0.5.2, (Robinson & Hayes 2019)), ‘siZer’ (version 0.1-5, (Sonderegger 2018)), ‘nlme’ (version 3.1-143 (Pinheiro & Bates 2000; Pinheiro et al. 2015)) and ‘MuMIn’ (version 1.43.15 (Barton 2019)).

2.6.2.2 Hypotheses 1 & 3: Surfacing behaviour & attitude

In order to compare the surfacing behaviour and attitude of healthy turtles and those with GE the variance in pressure values, pitch angles and roll angles were calculated for each turtle after one hour of tagging (the acclimatization period) over 1.5 and 24 hours. This was done to see if movement-based differences were immediately visible or evident throughout the course of a single day. The variance within the same three metrics (i.e., pressure, pitch and roll) was also evaluated during the first night post tagging (20:00–8:00) and the daylight hours following (8:00–20:00) to ascertain if convalescent and healthy turtles exhibited differing behaviour during these periods also. A Fisher's exact test of independence was conducted for each time period in order to see whether the variance in pitch and roll (in combination with VeDBA; see section 2.6.2.3) differed significantly between healthy and convalescent turtles. Fisher's tests, (conducted using the 'fisher.test' function within the R package 'stats' (Agresti 2002)) were used instead of Chi-squared tests; the former being preferable when sample sizes are small and one of the cells of the contingency table is below five (Bower 2003; McCrum-Gardner 2008).

2.6.2.3 Hypothesis 2: Activity

Potential differences in turtle movements were also assessed by way of VeDBA, a useful measure for activity that is commonly used as a proxy for energy expenditure for vertebrates in general (Gleiss et al. 2011; Halsey et al. 2011b) and turtles in particular (Enstipp et al. 2011; Halsey et al. 2011a). Daily activity profiles, comprised of histograms of VeDBA (Figure 2a, b) were drawn for each turtle using 24 hours of data (starting one hour after tagging). Values extracted from these histograms were analysed using an exponential decay function to extract the decay constant (Figure 2c, d; Appendix C, Figure C1). The daily activity profiles were based on 4-hour binning of the raw signals (returning four signals per hour). This level of binning is of a sufficiently high resolution for specific activity profile details, such as inflection points to be preserved. The exponential decay curves were drawn using a self-starting function 'SSasymp', which estimated its own start parameters (the Rstudio code used is provided below). This avoided the 'singular gradient' error which occurred when relying solely on the standard function for fitting non-linear equations, ‘nls’ (also from the R package ‘broom’ (Robinson & Hayes 2019)) if the estimate of rate constant, denoted here as ‘α_rc’, was poor). These ‘α_rc’ values were subsequently used in the comparison of activity profiles from healthy and GE recovering turtles.

The measured value, ‘y’ started at ‘y0’ and decayed towards ‘yf’ at a rate ‘α_rc’.

density = the proportion (or number of) data points per bin
breaks = the VeDBA values at each bin
yf = the end value on the x-intercept
y0 = the start value on the y-intercept
α_rc = the estimated decay rate constant

R code: nls(density ~ SSasymp(breaks, yf, y0, α_rc))

In order to examine observed inflection points in the 24-hour VeDBA distributions they were fit with bent-cable models using the ‘bent.cable’ function from the R package ‘siZer’ (Sonderegger 2018). The bent-cable comprises two straight lines joined smoothly by a quadratic bend in the middle. As the domain of the bend shrinks, the model approaches the widely used ‘broken stick’ model with an abrupt threshold between gradients (Chiu 2002). While fitting a broken stick (i.e., a piecewise linear model) requires an a priori abruptness assumption, fitting a bent-cable allows the observed data to reveal whether a sharp or smooth change is more convincing (Chiu 2002).

The ‘bent.cable’ function fits a model which is essentially a piecewise linear model with a quadratic curve of length 2γ (where γ is the half width of the transition zone) connecting the two linear pieces (Toms & Lesperance 2003; Sonderegger 2018). The bent-cable model is fit to the given data by searching the 2-dimensional parameter space to find the maximum likelihood estimators (MLEs) for alpha, i.e. the threshold or change point (henceforth denoted as ‘α_cp’ in order to distinguish it from the decay constant, ‘α_rc’ described above) and γ (Toms & Lesperance 2003; Chiu et al. 2006). If $\gamma = 0$, there is no transition zone (Toms & Lesperance 2003). In order to improve model fit and deal with potential multiple changes in slope, bent-cables were fitted to data that fell in between the upper (90%) and lower (10%) decile; this ensured that parameter estimation was based on the highest densities of underling data and removed the long tail of the histograms (Figure 2e–h).

2.6.2.4 Hypothesis 4: Angular velocity

Animal heading, expressed as the frequency of turn extents of 45°, 90°, 180° and 360° within one hour and mean hourly VeDBA was compared between healthy and convalescent turtles because this equated turn rate with movement activity (*cf.* hypothesis 4). Specifically, it highlights the extent to which acceleration-derived activity metrics are responsible for turns or are just acceleration *per se* (because, for example, animals can continue to attempt to swim without turning). Turn extent frequency and mean VeDBA were sampled at hourly intervals over a 24-hour period (starting one-hour post tagging); this generated 24 data points per turtle and took potential diurnal changes in behaviour into account. The relationship between turn extent and hourly VeDBA was assessed for each turtle *via* linear regression to examine if there were behavioural differences between healthy and recovering turtles.

Linear regressions were also used to assess the relationship between VeDBA, and three movement metrics related to turning: angular velocity, AAV and the differential angular velocity (movement metric units were in degrees/second). Angular velocity (derived from the combination of heading and yaw values formed on the surface of a sphere (Wilson et al. 2020b)), the AAV and the differential angular velocity (i.e. the rate of change of angles across the yaw axis) were smoothed over two seconds before being undersampled to 1 Hz (Gunner et al. 2020); hourly means were obtained from undersampled data spanning 24 hours, thus yielding 24 data points per individual.

2.6.2.5 Overall statistical analysis

A linear mixed-effects model (LMEM) was performed to see if turtle health status affected the relationship between mean VeDBA per hour and the number of turns per hour (equalling

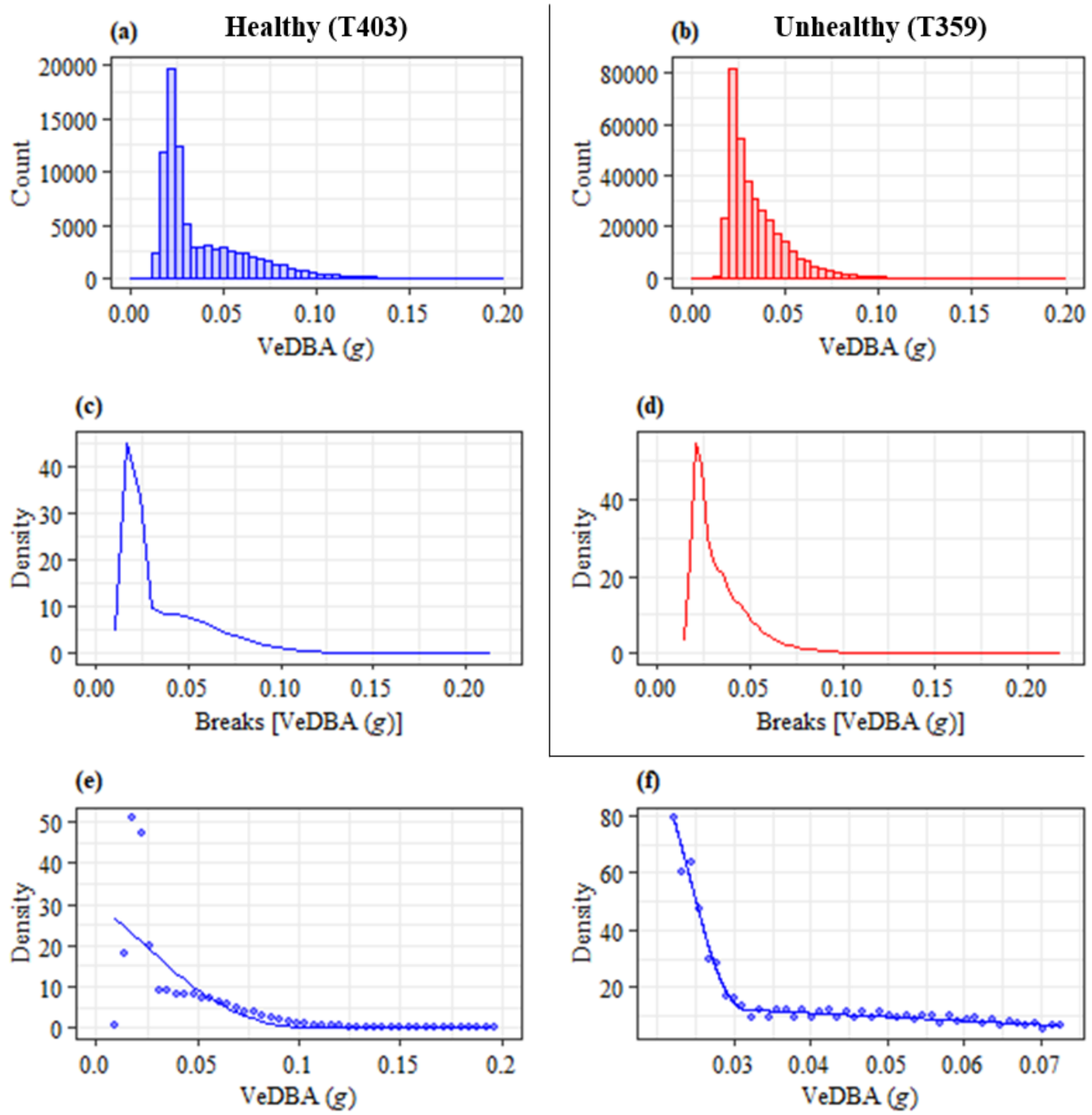


Figure 2. Examples of distributions of dynamic body acceleration (VeDBA) values during a 24-hour period for a healthy turtle (T403, cf. Table 1; depicted in blue) and a turtle recovering from gas emboli (T359, cf. Table 1; depicted in red). Panels (a) and (b) show the count frequencies of VeDBA values and panels (c) and (d) show the respective density plots. Note the point of inflection in the healthy turtle and the smooth curve in the unhealthy one. Bent-cable models fit with (e) the full 24-hours of data from T403 resulting in a poor model fit and (f) only the values that fell within the 10% and 90% quantiles of the 24-hour dataset, thus leaving one bend/changepoint in the data and improving model fit.

or surpassing a threshold of 45° within a five second window; see Figure 3). Hourly mean VeDBAs and 45° turn frequencies were calculated for each turtle over a 24-hour period (starting one-hour post tagging), yielding 24 data points per individual. Turn angles surpassing a threshold of 45° were used as they returned the highest R^2 of all the sampled thresholds; other sampled movement metrics related to turning, such as angular velocity, were not included in the model in order to avoid multicollinearity. Each turtle was either categorized as being 'healthy' (n = 20; the baseline point of reference) or recovering from GE (n = 9), according to veterinary assessment. A log transform was performed on the dependent variable, VeDBA, and independent variable, turn rate, to meet the assumption for a linear model. Turtle ID was incorporated into the model as a random effect to account for inter-individual differences such as turtle weight and sex. Tank size (i.e., an available water mass of 1,500 L, 3,000–3,500 L, 6,000–7,000 L or 19,000 L), was initially incorporated as a fixed effect to account for any associated confounding effects; it did not significantly affect VeDBA and was subsequently removed when determining the best fitting model through forwards stepwise selection and Akaike Information Criterion (AIC).

The LMEM (R code below) was conducted using the 'lme' function from the 'nlme' package in R (Pinheiro & Bates 2000; Pinheiro et al. 2015) and included the 'varIdent' function (Gałecki & Burzykowski 2013), to allow for heterogeneity of variance between individuals which was indicated by model diagnostic plots. The 'summary' function was used to extract *p*-values, thus giving a measure of significance for each of the coefficient estimates. Marginal and conditional R^2 values for model goodness-of-fit were obtained *via* the 'r.squaredGLMM' function within the 'MuMIn' package (Barton 2019): the marginal R^2 indicated the variance explained by fixed factors, and conditional R^2 indicated the variance explained by both fixed and random factors (Nakagawa & Schielzeth 2013).

R code:

```
lme(log.VeDBA ~ log.turn45 + condition, random = (~1 |Turtle.ID), weights =
    varIdent(form = ~1 | Turtle.ID), control=ctrl, data = data)
```

The magnitude of dependence in scores attributable to differences between turtles (turtle ID) was calculated using the intraclass correlation coefficient (ICC). This was estimated as proportion of variance in the dependent variable (VeDBA) resulting from turtle ID, to total variance, where σ_{τ}^{2} was the estimated turtle variance and σ_{ε}^{2} was the estimated residual variance (Kenny & Hoyt 2009).

$$ICC = \frac{\sigma_{\tau}^{2}}{\sigma_{\tau}^{2} + \sigma_{\varepsilon}^{2}}$$

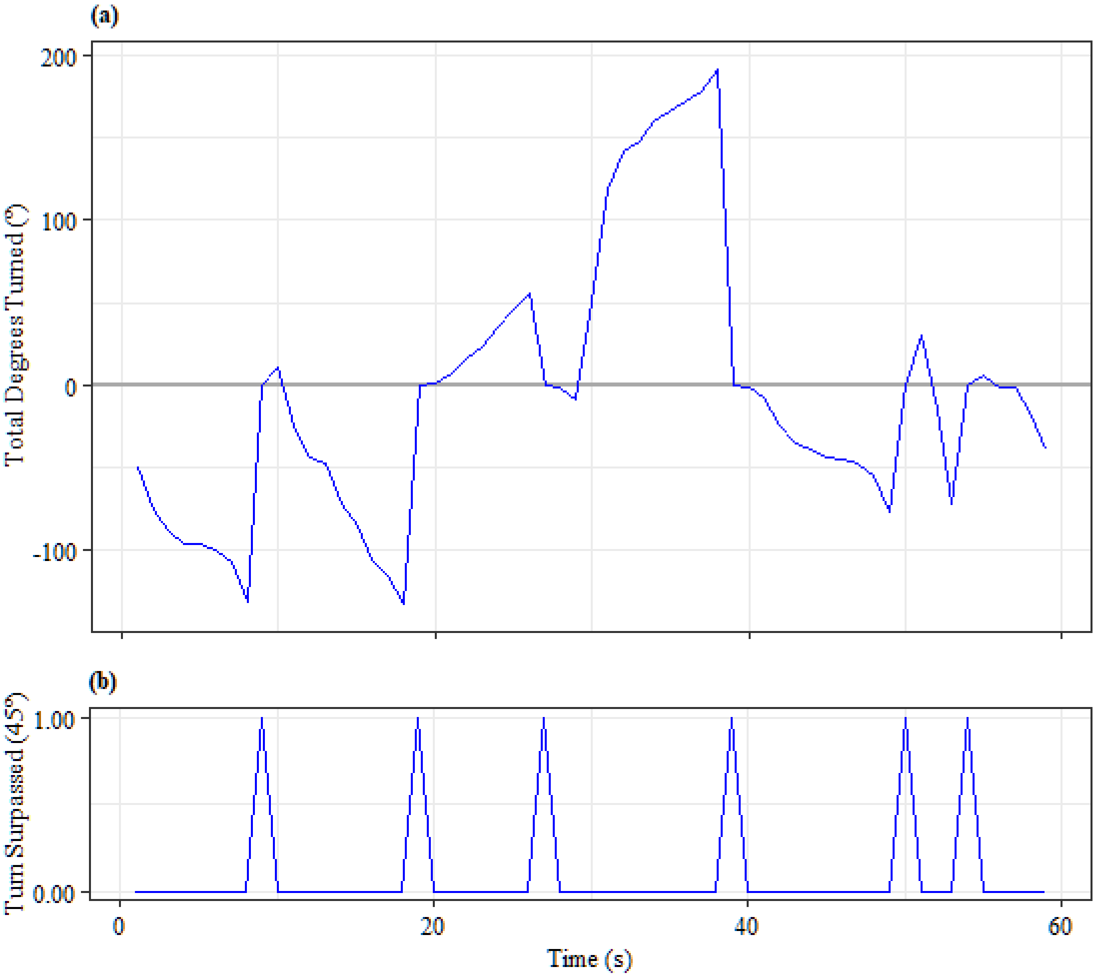


Figure 3. Example tag data from a turtle during a one-minute period showing (a) the total degrees turned towards the left and the right and (b) each time a 45° threshold was surpassed within a five second window; the spikes indicate that this occurred six times. Magnetic heading, used to calculate the number of turns, was undersampled to 1 Hz.

3. Results

On the date of tagging, 20 of the 29 turtles included in this study were healthy and nine were recovering from GE of varying severity (mild n = 2, moderate n = 5 and severe n = 2; see Table 1). The nine recovering turtles were categorized as ‘convalescent’ and were tagged after treatment and upon initial release into a rescue centre tank, 1–2 days after admission to the rehabilitation centre. All study animals were small to large juveniles (ranging from 31–64 cm CCL and weighing 3.24–41.28 kg) except T234, an adult female measuring 83 cm CCL and weighing 85.5 kg.

3.1 Surfacing behaviour

The surfacing behaviour and consequently the depth profiles of healthy and convalescent turtles appeared to differ with healthy turtles resting on the tank floor and ascending to breathe roughly every 10–20 minutes (resulting in a bimodality in pressure values; Figure 4a) and convalescent turtles surfacing more regularly and lacking the clear rest/bottom periods (resulting in a wider spread in pressure values; Figure 4b). However, there was considerable overlap in the pressure variance values obtained from healthy and unhealthy individuals across all timeframes; over 1.5 hours (Figure 4c), over 24 hours (Figure 4d), during the first night post-tagging (Figure 4e) and the daylight hours following (Figure 4f). Convalescent turtles tended to present more extreme values of pressure variance, especially over a 24-hour period and during the day.

3.2 Activity based on VeDBA alone

Turtle activity, as indicated by mean VeDBA over 24 hours, showed no clear links with turtle weight, curved carapace length (CCL) or condition, i.e., whether an individual was healthy or convalescent (Figures 5 and 6). The prediction that VeDBA should vary with health status (*cf.* hypothesis 2), was not upheld. The decay constant (α_rc), from the exponential curve fits, showed considerable overlap between healthy and convalescent turtles (Figure 7a–d and 8a). Similarly, bent-cable models fitted to the 24-hour data, yielding maximum likelihood estimators (MLEs) for

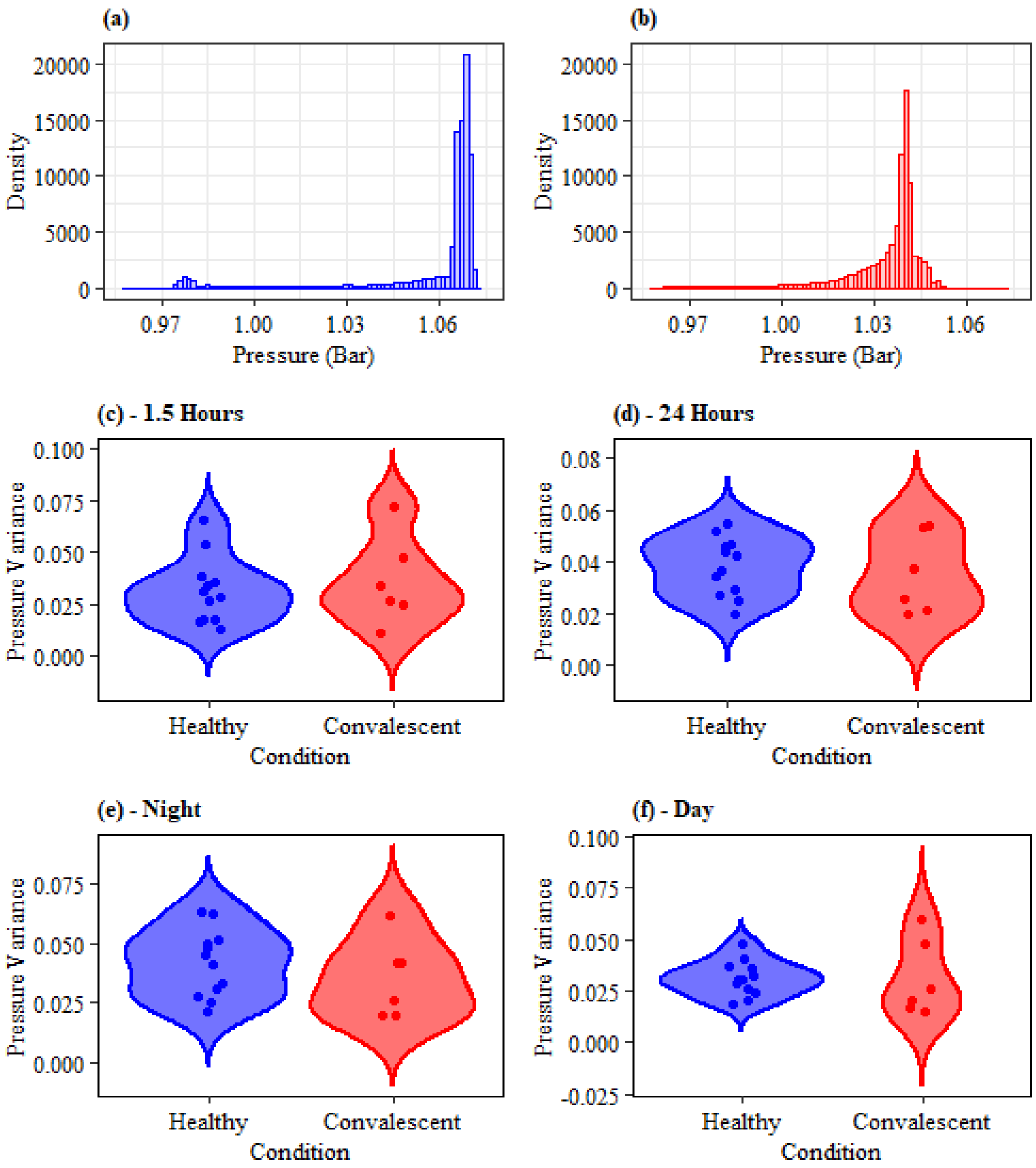


Figure 4. Pressure data from healthy turtles (depicted in blue) and turtles recovering from gas emboli (depicted in red). Pressure profiles during a 24-hour period in a (a) healthy turtle (T404 cf. Table 1) and (b) a turtle recovering from gas emboli (T383 cf. Table 1). Note the small hump at low pressure and the large peak at high pressure for the healthy turtle (this distribution resulting from momentarily surfacing to breathe and then resting on the tank floor) and the wider solitary peak indicating time spent at varying depths for the recovering turtle. Violin plots show the variance in pressure for healthy (n = 12) and convalescent (n = 6) turtles for periods of (c) 1.5 hours, (d) 24 hours, (e) at night (20:00–8:00) and (f) during the following day (8:00–20:00). There was considerable overlap in pressure variance between healthy and convalescent turtles across all timeframes, although the latter generally displayed a greater range in values, indicating greater inter-individual differences, in particular over a 24-hour period and during the day.

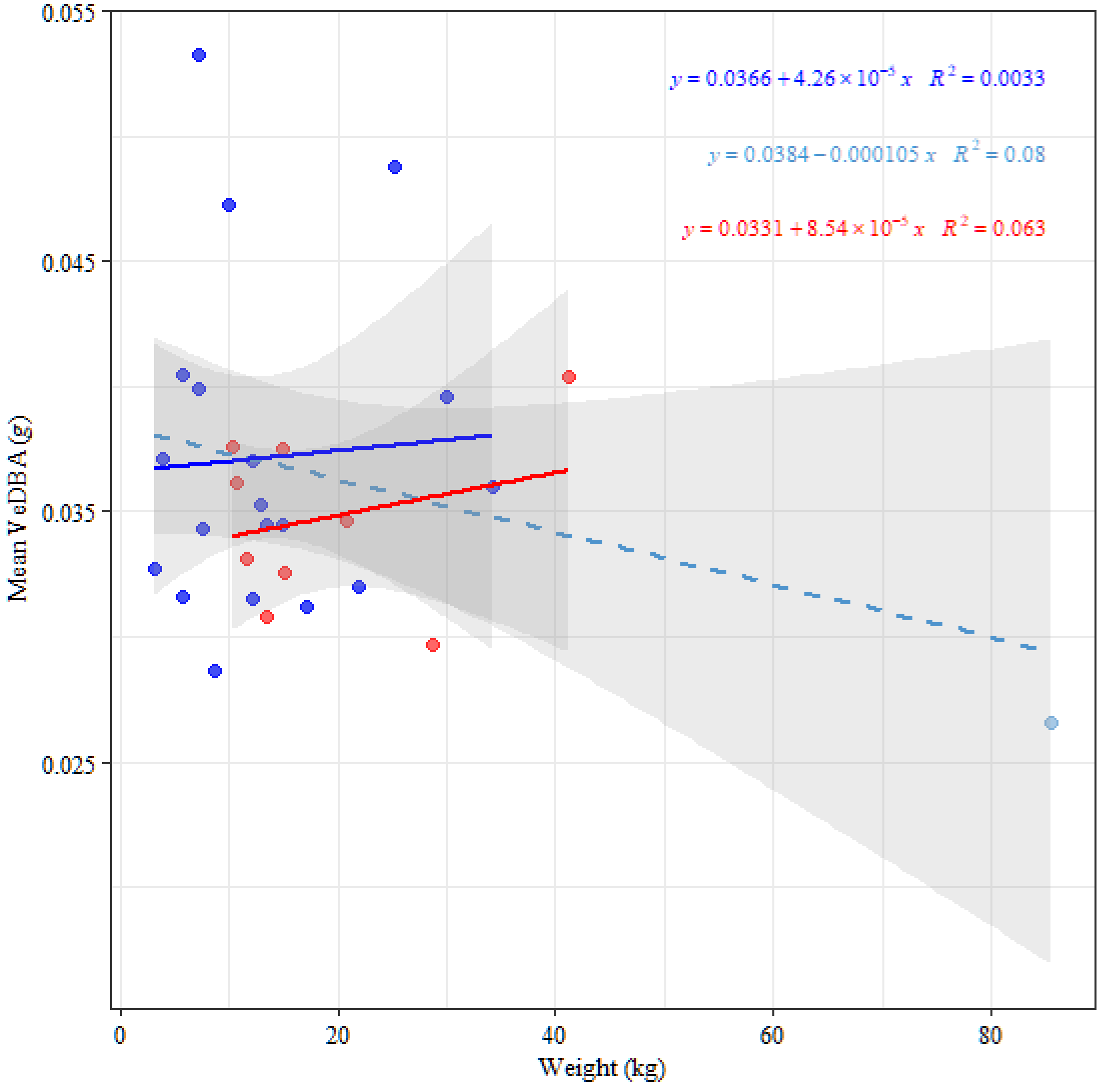


Figure 5. Relationship between turtle weight (kg) and mean VeDBA (g) smoothed over two seconds; each point represented 24 hours of tag data collected from a turtle. Convalescent turtles (i.e., recovering from gas emboli; n = 9), were coloured red and healthy turtles (n = 20) were coloured blue, including an outlier that was coloured in light blue. Regression lines were drawn for convalescent turtles (in red) and healthy turtles, both with and without the outlier (shown in light blue and blue respectively); grey shading either side of regression lines indicated 95% confidence intervals. No clear relationship between activity and weight related to condition (i.e., whether a turtle was healthy or convalescent) was apparent.

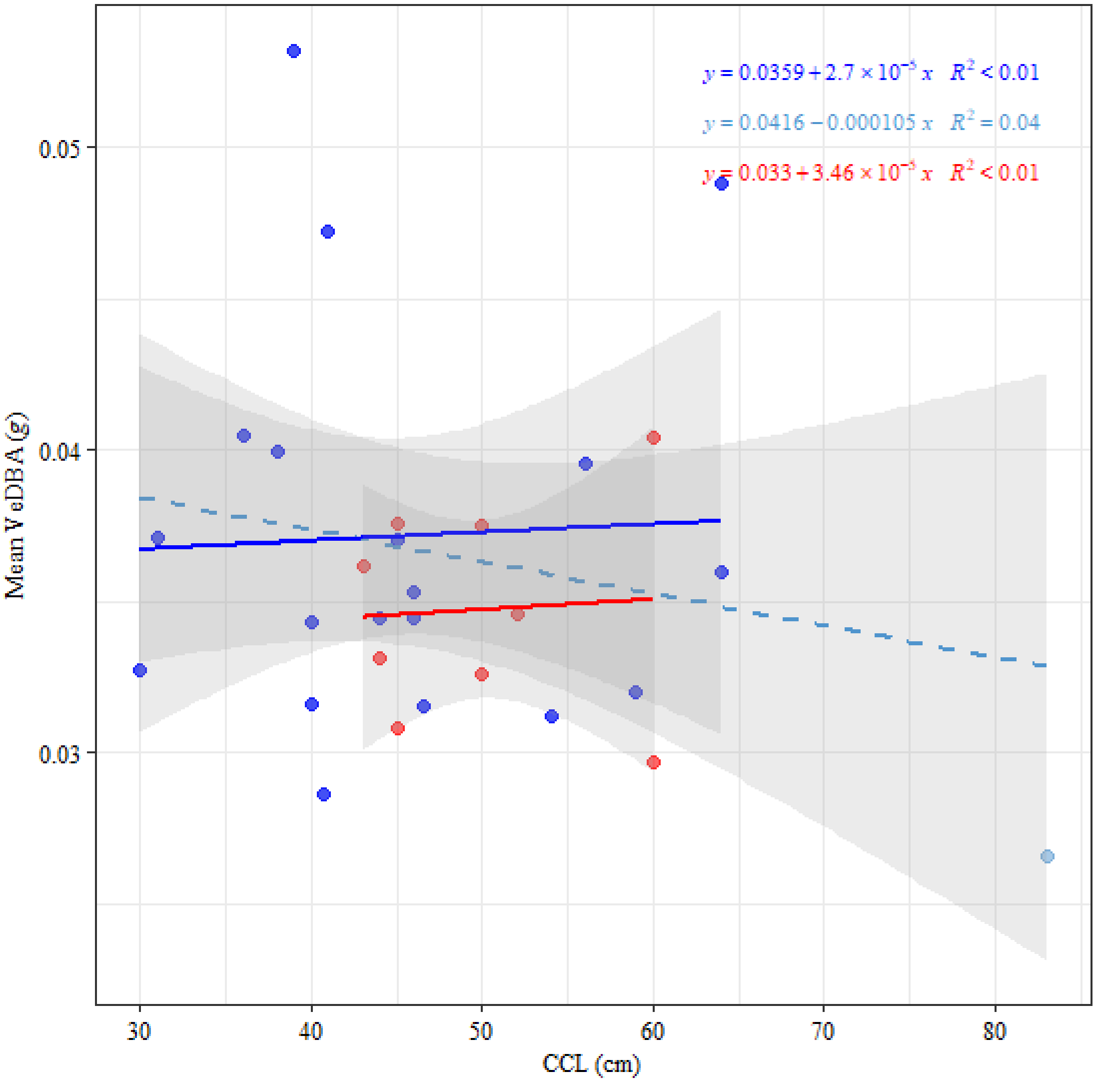


Figure 6. Relationship between curved carapace length, CCL (cm) and mean VeDBA (g) smoothed over two seconds; each point represented 24 hours of tag data collected from a turtle. Convalescent turtles (i.e., recovering from gas emboli; n = 9), were coloured red and healthy turtles (n = 20) were coloured blue, including an outlier that was coloured in light blue. Regression lines were drawn for convalescent turtles (in red) and healthy turtles, both with and without the outlier (shown in light blue and blue respectively); grey shading either side of regression lines indicated 95% confidence intervals. No clear relationship between activity and CCL related to condition (i.e., whether a turtle was healthy or convalescent) was apparent.

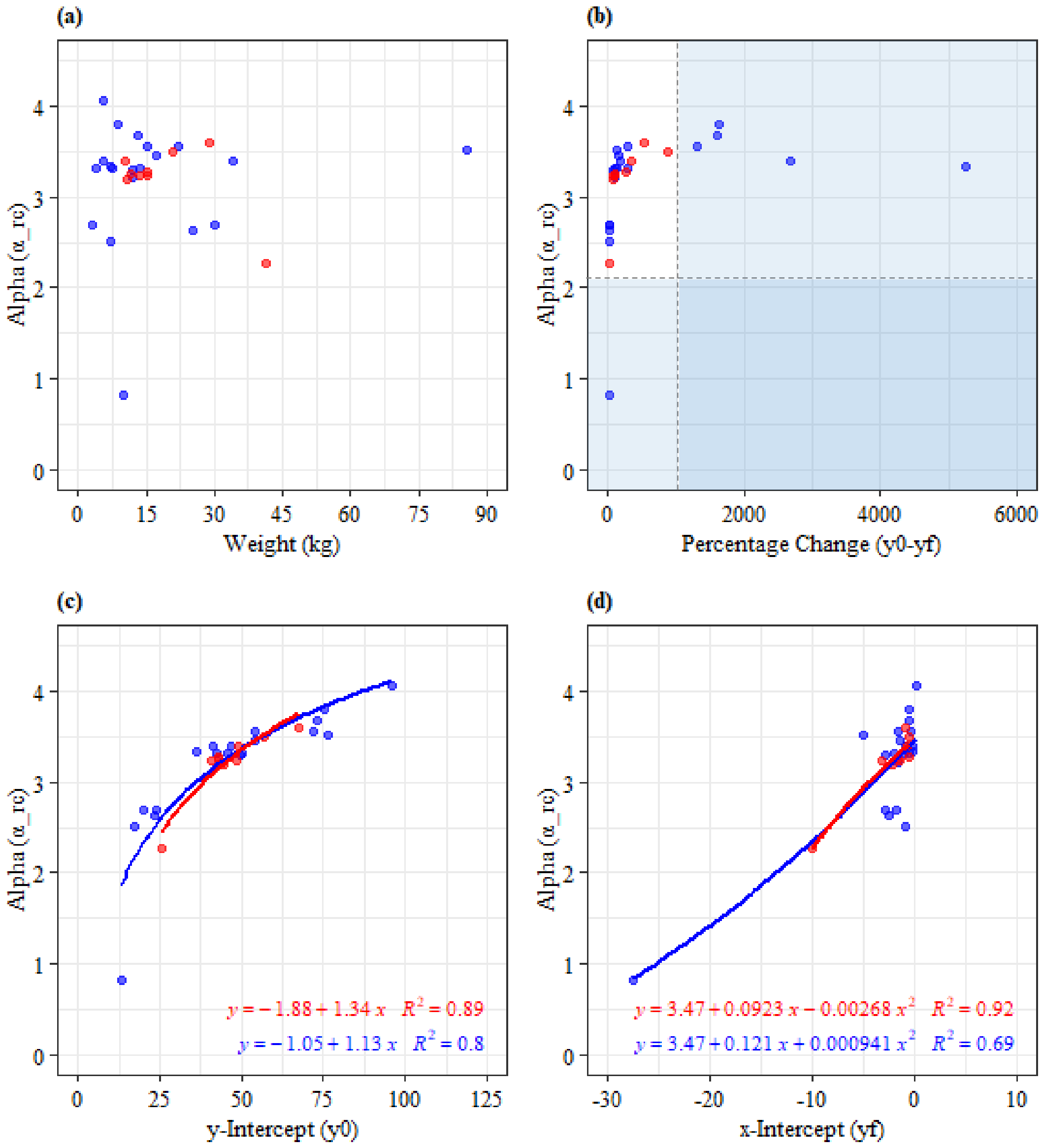


Figure 7. Results from exponential decay curves, fit to VeDBA distributions of turtle tag data collected during a 24-hour window; plots show (a) turtle weight (kg) against the rate of decay constant 'α_rc', (b) the percentage change from the y-intercept 'y0' to the x-intercept 'yf' against 'α_rc', (c) the y-intercept 'y0' against 'α_rc' and (d) the x-intercept 'yf' against 'α_rc'. Each blue point represented a healthy turtle (n = 18) and each red point, a convalescent turtle (n = 9). The dotted lines in (b) indicate the area in which convalescent turtles were confined to (not shaded), two areas where only healthy turtles occurred (light shading) and an area with no turtles (darker shading). The spread in decay constant values was greater for healthy turtles, indicating greater inter-individual variability in activity, consequently all recovering turtles fell within the healthy turtle range, thus making the decay constant an unsuitable metric for the discernment of turtle health status.

α_cp (the threshold or change point value; Figure 8b) and γ (the half width of the transition zone; Figure 8c): MLEs showed no clear differences between turtles of differing health status.

3.3 Pitch and roll distributions

Despite the hypothesis that GE related injuries may impair manoeuvrability and lead to instability, resulting in greater variation in body attitude (pitch and roll) than in healthy animals, (*cf.* hypothesis 3; Figure 9a–d), the variance in pitch and roll when graphed against the variance in VeDBA revealed broad coherence between both groups for all of the periods considered: over 1.5 and 24 hours respectively (Figure 10a, e and Figure 10b, f), during the first night post tagging (Figure 10c, g) and during the daylight hours following this (Figure 10d, h). The same set of graphs were also drawn with mean VeDBA instead of VeDBA variance (Appendix D, Figure D1). For both the VeDBA variance and mean VeDBA sets of graphs, and across all timeframes, all points in the top right-hand corner of graphs (representing higher variance) were exclusively derived from healthy turtles.

The probability of a healthy turtle having a higher variance in VeDBA (Figure 10a–c) or VeDBA-pitch/VeDBA-roll combination (Figure 10d and Figure 10e–h respectively) was significant for all timeframes except 1.5 hours (corresponding Fisher's exact test results, shown on each graph in Figure 10, include *p*–values, odds ratios and 95% confidence intervals). Note that the greatest significance was observed during the day where the probability of a healthy turtle having a VeDBA above 0.00024 *g* and pitch variance above 200 (i.e., that fell outside of the unshaded area; Figure 10d) was 16.7 times that of a convalescent turtle (95% CI[1.659, 880.325], $p = 0.005$). Similarly, the probability of a healthy turtle having a VeDBA above 0.00021 *g* and roll variance above 140 (Figure 10h) was 15.5 times that of a convalescent turtle (95% CI[1.792, 230.816], $p = 0.004$).

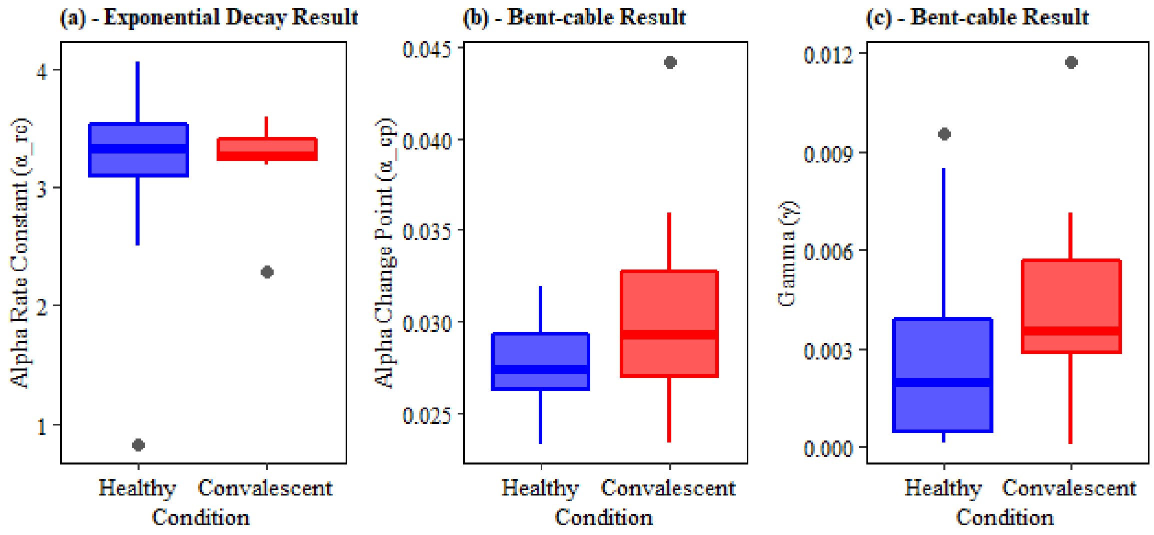


Figure 8. Results from (a) exponential decay curves and (b,c) bent-cable models that were fit to healthy turtle (n = 18; depicted in blue) and unhealthy turtle (n = 9; depicted in red) activity distributions that were based on VeDBA values and covered 24-hour periods. Boxplots indicate the spread of (a) rate of decay constant alpha, 'α_rc' values and maximum likelihood estimators (MLEs) for (b) the change point, denoted by 'α_cp' and (c) the half width of the transition zone, gamma, 'γ'. Bent-cables were fitted to data recorded over a 24-hour period that fell in between the upper (90%) and lower (10%) decile. The spread in α_rc values was greater for healthy turtles, thus indicating a higher degree of variability in the transition from low to high VeDBAs among healthy individuals. Similarly, γ values from healthy turtles also covered a wider spread, albeit minor. Conversely, change point 'α_cp' values varied less, potentially indicating a more definitive inflection point within the healthy turtle group. Bent-cable MLEs indicated that healthy turtles tended to have slightly lower α_cp and γ values. Nonetheless the overlap across all healthy and convalescent turtle boxplots indicated that particular activity patterns were not unique to either group.

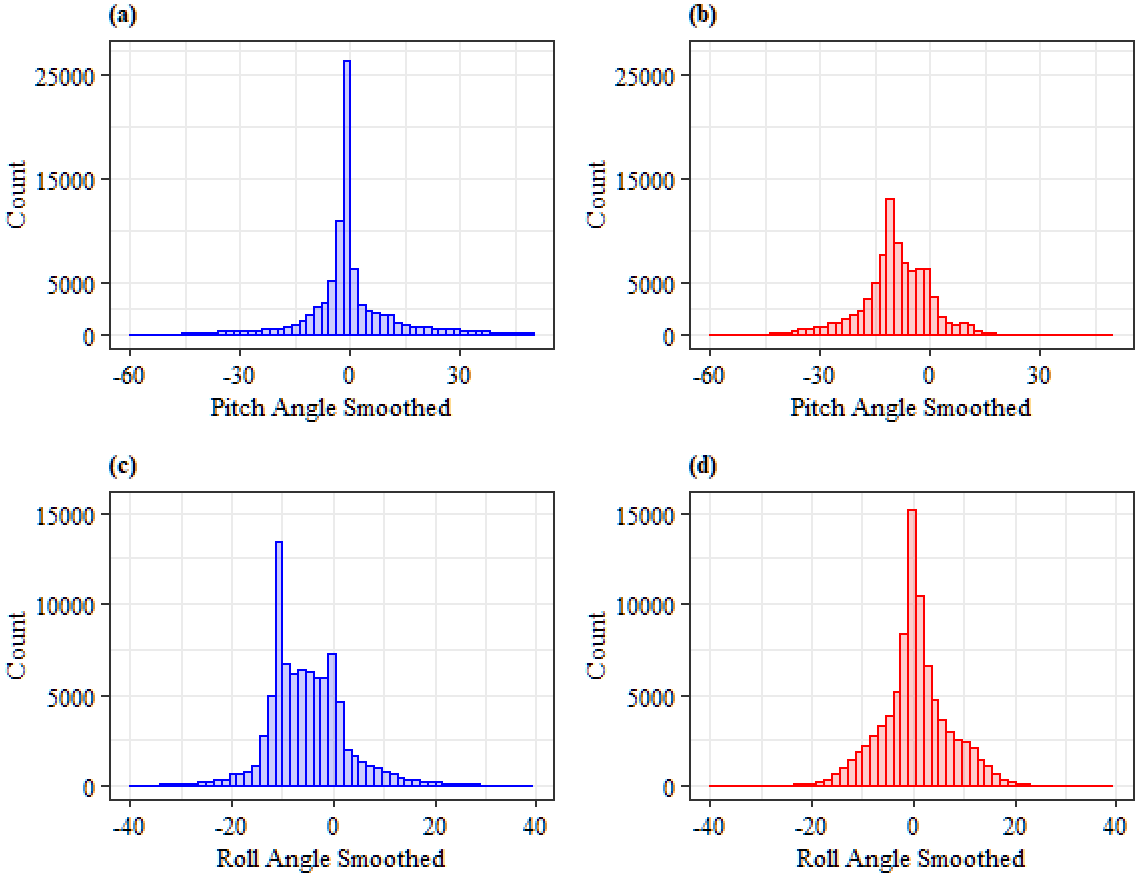


Figure 9. Distribution of (a, b) pitch and (c, d) roll angles over a 24-hour tagging period in (a, c) a healthy turtle in blue (T403 cf. Table 1) and (b, d) a convalescent turtle in red (T443 cf. Table 1). Note the narrow peak in healthy turtle pitch values, indicating time devoted to a particular attitude (for example resting on the tank floor) compared to the wider spread in convalescent turtle values, indicating time spent at various attitudes. Roll angle, however, was more varied in the healthy turtle, suggesting time spent with the body tilted sideways (left and right), perhaps whilst swimming or resting by the side of the tank. The narrow, central peak in convalescent turtle roll values shows that the majority of time was spent in one plane, the tapering ends may signal a lack of control when in a tilted position and the tendency to self-right.

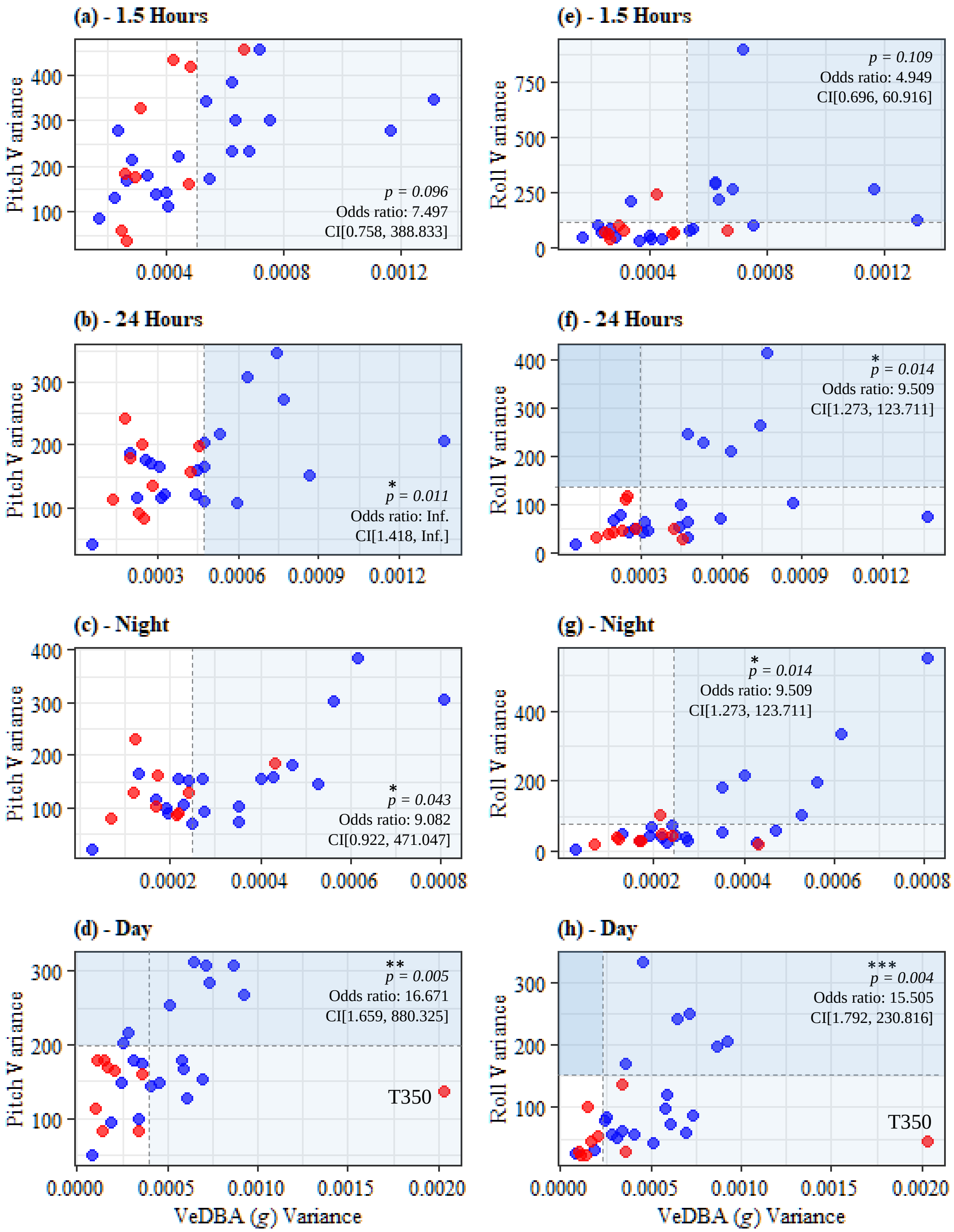


Figure 10. Variance in VeDBA (g) per turtle against variance in pitch (a–d) and roll (e–h) for healthy turtles (in blue; n = 18) and convalescent turtles (in red; n = 9). Variance in pitch and roll was calculated over periods of (a, e) 1.5 hours, (b, f) 24 hours, (c, g) at night (20:00–8:00) and (d, h) during the day (8:00–20:00). Values from convalescent turtles generally fell within the healthy turtle range; however, all points

in the top right-hand corner of graphs, with a higher variance, were exclusively from healthy turtles. The dotted lines defined areas where healthy and convalescent turtle values overlapped (not shaded), areas with a majority of healthy turtles and only one or two convalescent turtles (light shading), areas exclusive to healthy turtles (medium shading) and areas with no turtles (darker shading). Using these defined areas, Fisher's exact test were conducted; results were displayed on each graph showing the statistical significance, the odds ratio, and the 95% confidence interval [CI]). For all timeframes except 1.5 hours, the probability of a healthy turtle having a higher, (i.e., outside the unshaded area) VeDBA (graphs a, b, c) or VeDBA-pitch/VeDBA-roll combination (graph d and graphs e–h respectively) than a convalescent turtle, was significant.

3.4 Turns per hour and angular velocity

No relationship was found between turning behaviour and turtle weight, CCL or condition, i.e., whether an individual was healthy or convalescent (Figures 11 and 12). Linear regressions revealed that the turning rate for convalescent turtles was generally higher than for healthy animals across all thresholds 45°, 90°, 180° and 360° (Figures 13 and 14). Regressions showing the relationship between mean VeDBA against the four sampled turn angles for all turtles in Table 1 are available in Appendix E, Figures E1–8. R^2 values, obtained from linear regressions of mean VeDBA and the number of turns per hour, indicated that the model goodness-of-fit was higher in healthy turtles for all sampled turn thresholds except 360° (Figure 14e and Figure 15).

As with turn rate and mean VeDBA, the relationship between angular velocity and mean VeDBA increased faster in convalescent turtles than in healthy turtles (Figure 16a). However, no health status related differences were found between mean VeDBA and the AAV (Figure 16b) or VeDBA and the differential angular velocity (Figure 16c).

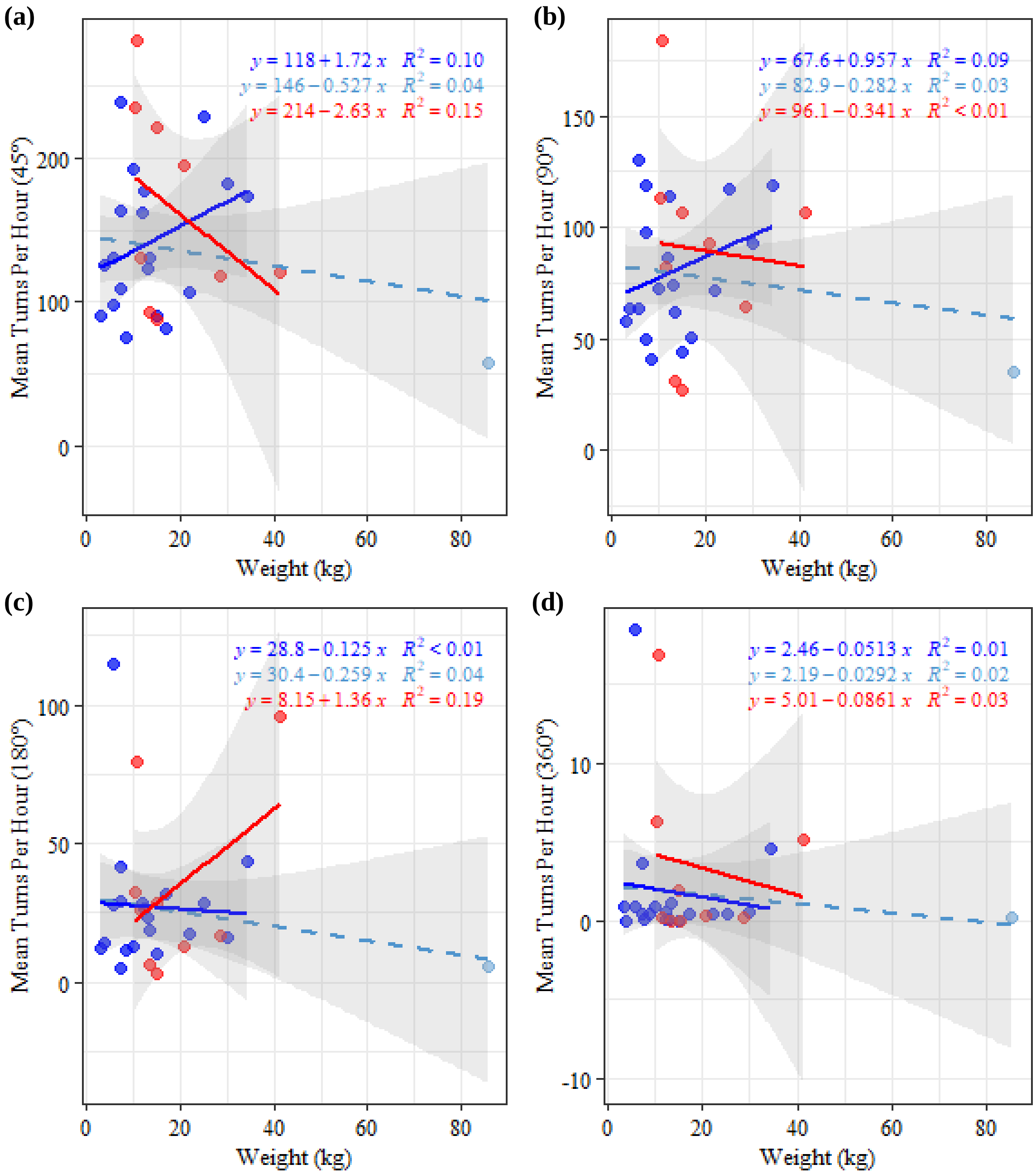


Figure 11. Relationship between turtle weight (kg) and total turns per hour at angle thresholds of (a) 45°, (b) 90°, (c) 180° and (d) 360°, smoothed over two seconds; each point represented 24 hours of tag data collected from a turtle. Convalescent turtles (i.e., recovering from gas emboli; n = 9), were coloured red and healthy turtles (n = 20) were coloured blue, including an outlier that was coloured in light blue. Regression lines were drawn for convalescent turtles (in red) and healthy turtles, both with and without the outlier (shown in light blue and blue respectively); grey shading either side of regression lines indicated 95% confidence intervals. No clear relationship between turning and weight related to condition (i.e., whether a turtle was healthy or convalescent) was apparent.

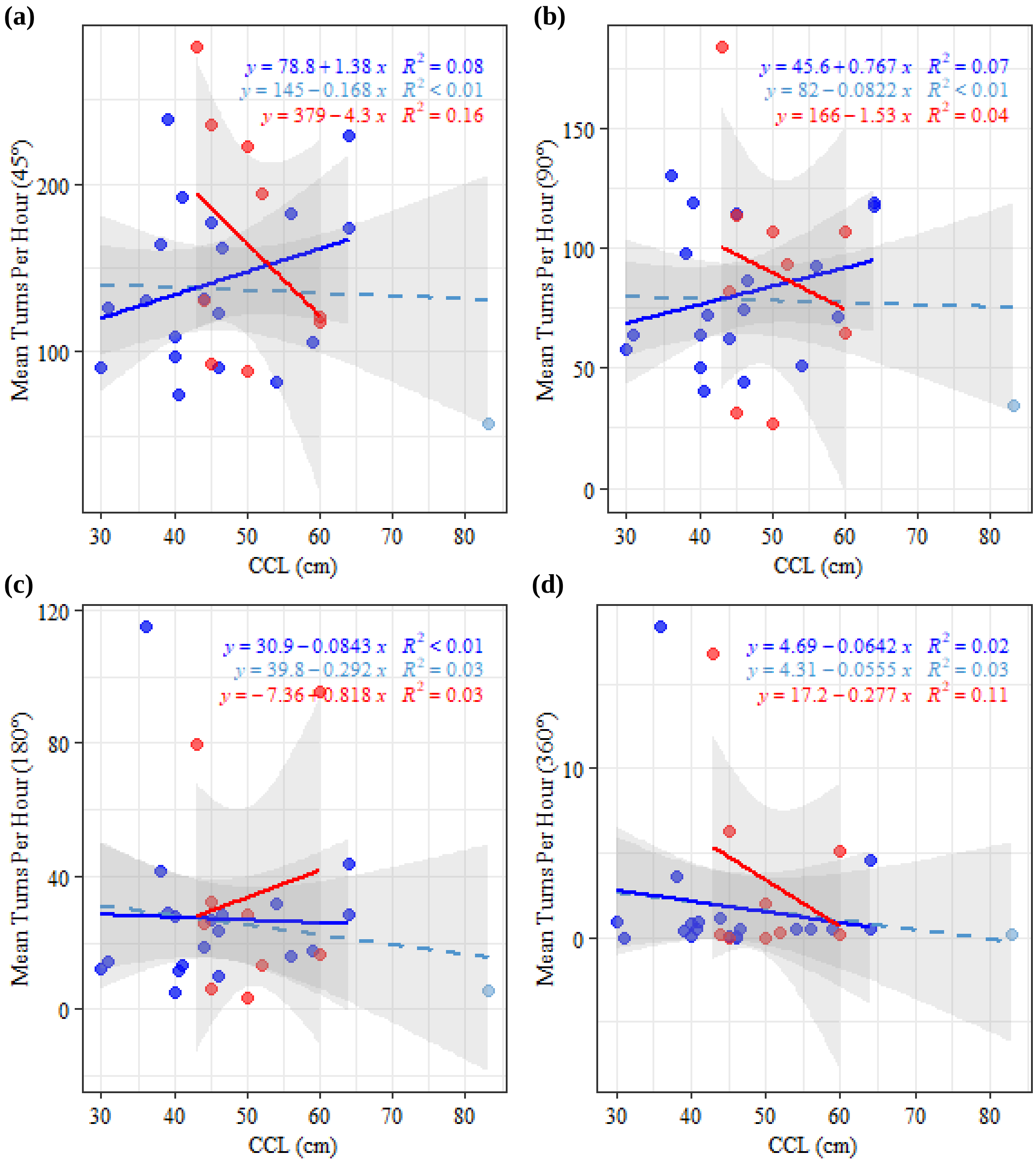


Figure 12. Relationship between curved carapace length, CCL (cm) and total turns per hour at angle thresholds of (a) 45°, (b) 90°, (c) 180° and (d) 360°, smoothed over two seconds; each point represented 24 hours of tag data collected from a turtle. Convalescent turtles (i.e., recovering from gas emboli; n = 9), were coloured red and healthy turtles (n = 20) were coloured blue, including an outlier that was coloured in light blue. Regression lines were drawn for convalescent turtles (in red) and healthy turtles, both with and without the outlier (shown in light blue and blue respectively); grey shading either side of regression lines indicated 95% confidence intervals. No clear relationship between turning and CCL related to condition (i.e., whether a turtle was healthy or convalescent) was apparent.

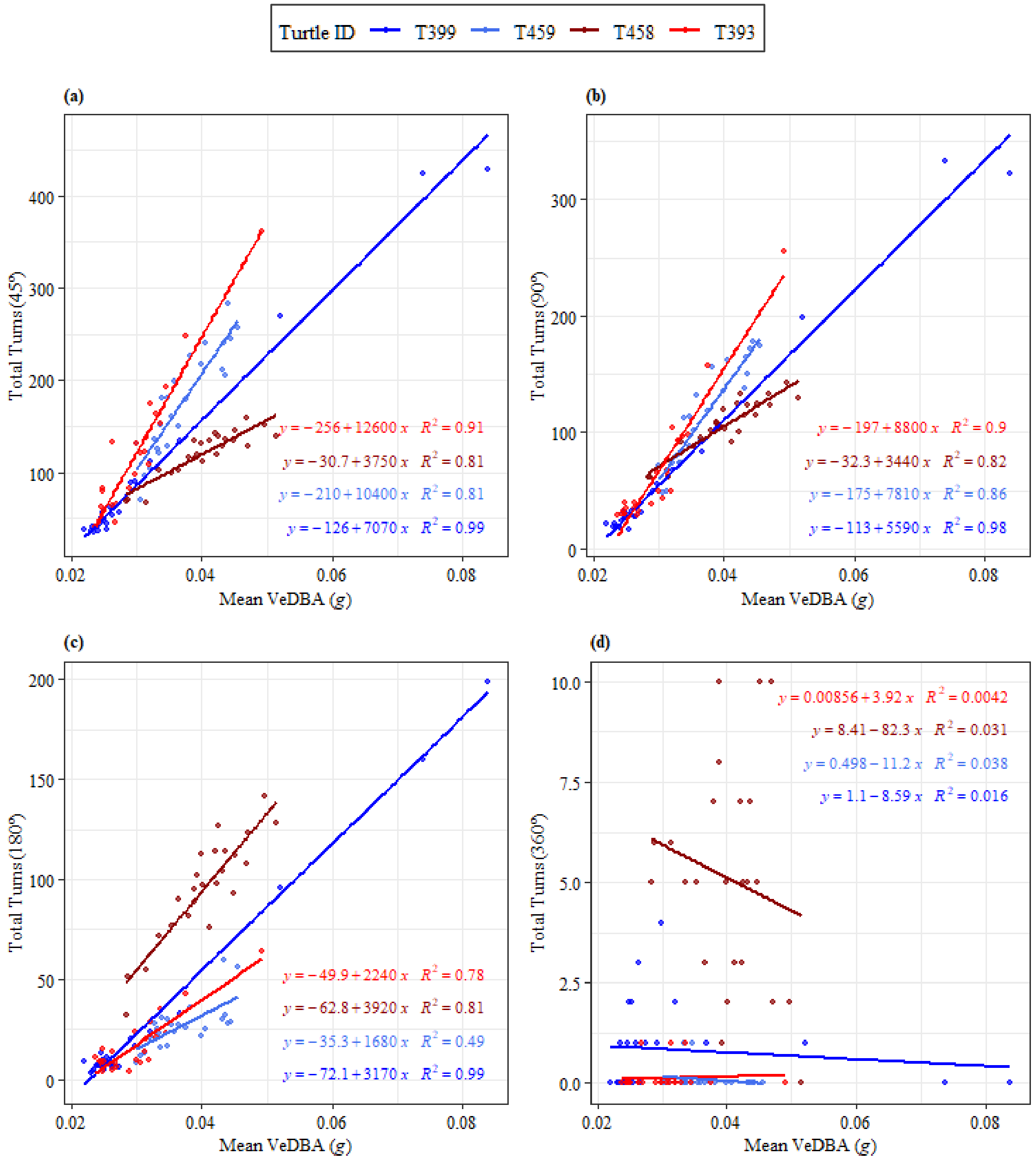
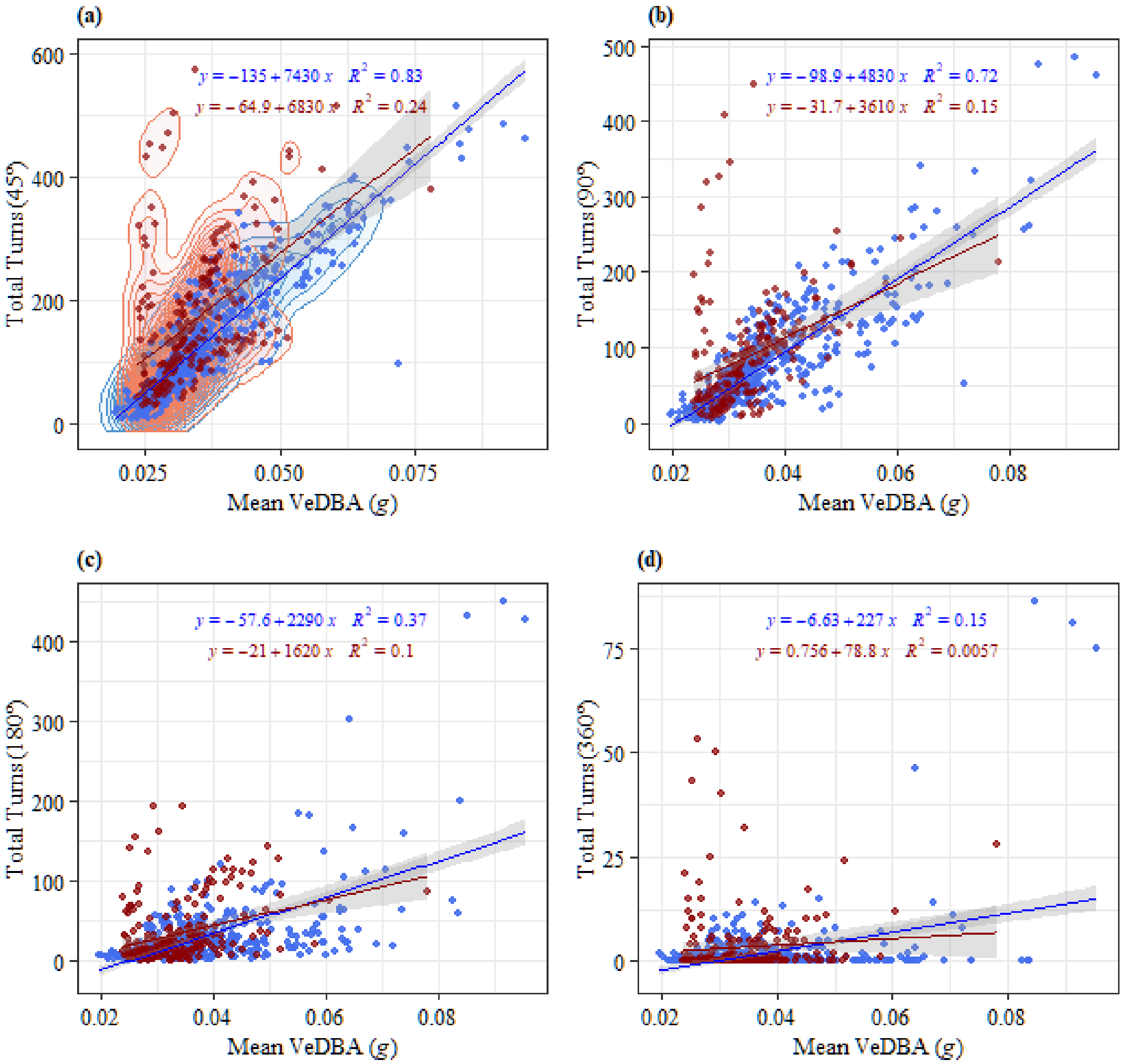


Figure 13. Linear regressions of mean VeDBA and the total number of turns per hour surpassing turn angle thresholds of (a) 45°, (b) 90°, (c) 180° and (d) 360°, in four example turtles using tag data covering a 24-hour period. Two healthy turtles were shown in blue and two convalescent turtles were coloured red (see Table 1 for detail on turtles in legend). Graphed linear regressions for all of the turtles in Table 1, at each of the sampled turn angles (i.e., 45°, 90°, 180° and 360°) have been included in Appendix E, Figures E1–8.



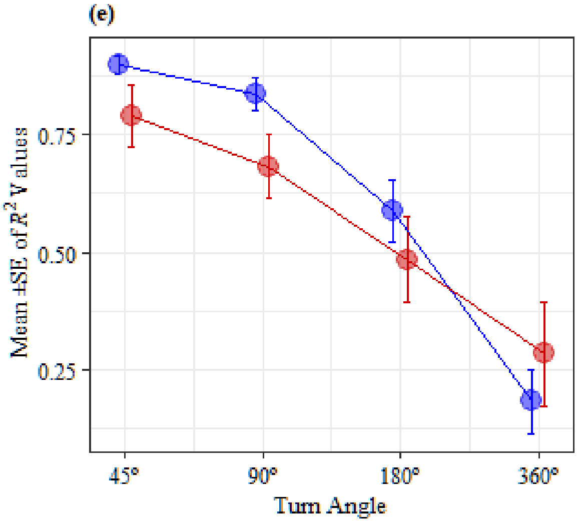


Figure 14. Relationship between mean VeDBA (g) and the mean number of turns per hour that surpassed (a) 45°, (b) 90°, (c) 180° and (d) 360°. Each data point represented one hour of data collected during the 24-hour tagging period, resulting in 24 data points per turtle. Points and regression lines were colored according to turtle condition (convalescent, i.e., recovering from gas emboli = red;

Healthy = blue); 95% confidence intervals were indicated by the grey shading either side of regression lines. Line gradients indicated that the mean VeDBA and number of turns per hour was higher in convalescent turtles. (e) Mean ±SE of R² values at each of the sampled turn angles for healthy turtles (in blue) and convalescent turtles (in red). The former generally had a higher R² for all angles except 360° where the relationship broke down as turtles seldom completed a full turn.

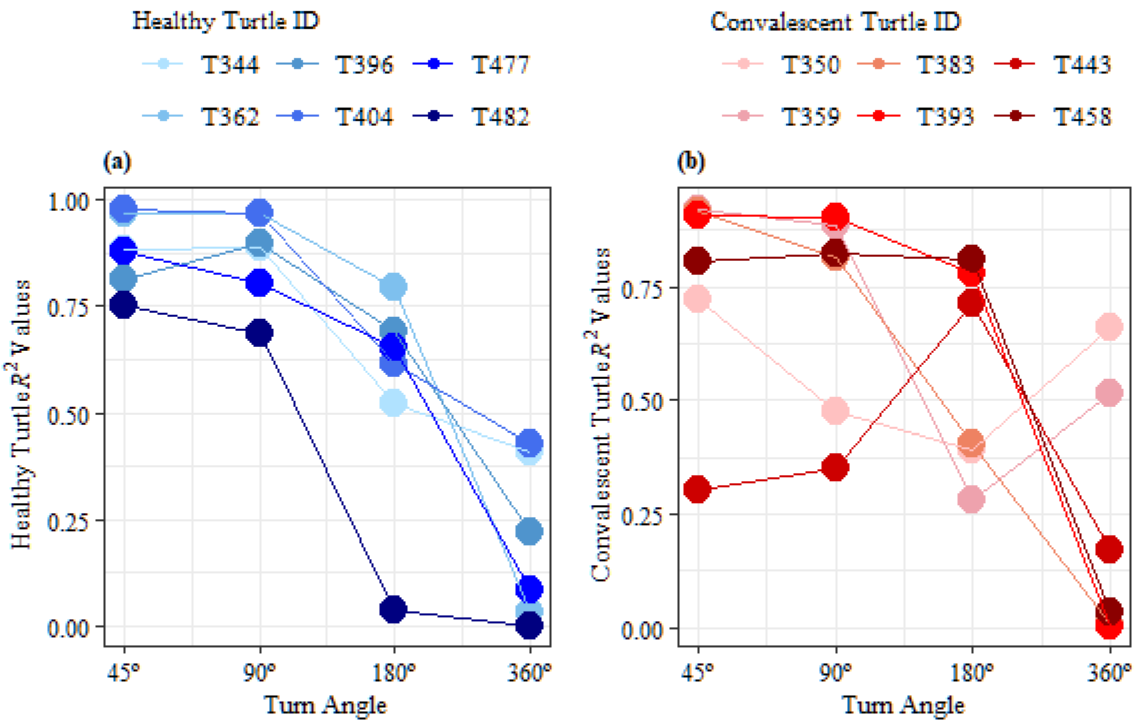
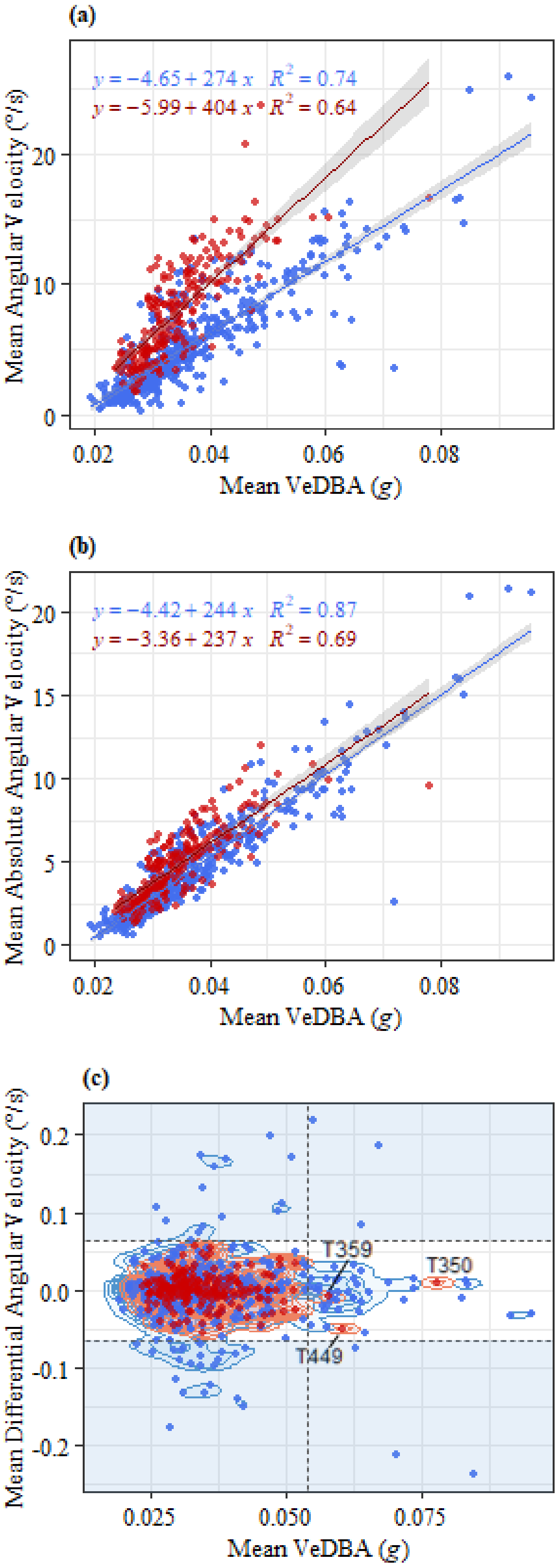


Figure 15. R² values obtained from linear regressions of mean VeDBA and the number of turns per hour (at 45°, 90°, 180° and 360°) over a 24-hour period in (a) six healthy turtles shown in shades of blue and (b) six convalescent turtles in shades of red (see Table 1 for detail on turtles in legend).

Figure 16. Mean VeDBA (g) against (a) mean angular velocity in the yaw plane, (b) the mean Absolute Angular Velocity (AAV), and (c) the mean differential of angular velocity. All parameters on the y-axis were smoothed over one second (20 Hz) and means were calculated at hourly intervals for a 24-hour period (giving 24 data points per turtle), beginning after a one-hour acclimatization period. Healthy turtles (n = 20) are coloured blue and unhealthy turtles (n = 9) are coloured red. Note that mean angular velocity regression lines for healthy and unhealthy turtles diverge, whereas mean AVV lines do not. The contour lines in (c) indicate kernel density; the dotted lines about the non-shaded area indicate where convalescent turtle values were clustered. Convalescent turtles all had low differential angular velocity values (within the central non-shaded area), and generally low mean VeDBAs (with the exception of three outliers– the turtle ID for each is shown on the graph). The top and bottom bands with no convalescent turtles were shaded darker for clarity. Note that greater differentials, both positive and negative (i.e., > 0.065 or < -0.055), were only recorded in healthy turtles.



3.5 Overall statistical analysis

The linear mixed-effects model (LMEM) incorporating all covariates (turn rate, turtle condition and turtle ID; Table 2), yielded the best goodness-of-fit (marginal $R^2 = 0.49$; conditional $R^2 = 0.65$). The number of 45° turns per hour significantly affected VeDBA (LMEM: $\chi^2_{(33)} = 7.266$, $p < 0.007$); for every 10% increase in turn rate, VeDBA increased by 3% (Est. = 0.29 ± 0.00 (S.E), t = 58.27, 95% CI[0.279, 0.299], $p < 0.0001$). Turtle condition, when convalescent, had a significant negative effect on VeDBA (Est. = -0.14 ± 0.06 (S.E), t = -2.77, 95% CI[-0.236, -0.035], $p = 0.010$). The intraclass correlation coefficient (ICC) estimated the proportion of variance in VeDBA resulting from turtle ID; the ICC was low (0.40), indicating low similarity between values from the same group (n = 29).

Table 2. Linear mixed-effects model (LMEM) estimates of fixed effects, p-values and 95% confidence intervals for mean VeDBA/hour. The analysis was performed to see if turtle condition (healthy or convalescent) affected the relationship between the number of turns per hour (surpassing a threshold of 45°), the mean angular velocity (°/s) and mean VeDBA per hour during the first 24 hours of tag attachment.

Variable	**Est.**	**S.E.**	***t*-value**	**D.F.**	**95% CI**	***p*-value**
Intercept	-4.69	0.04	-131.12	666	[-4.765, -4.624]	0.000
Log turns/hour (45°)	0.29	0.00	58.27	666	[0.279, 0.299]	0.000
Convalescent	-0.14	0.05	-2.77	27	[-0.236, -0.035]	0.010

4. Discussion

The purpose of this study was to examine the value of animal-attached movement-sensitive tags to discriminate between healthy- and GE-affected turtles because, if successful, tag-derived behavioural biomarkers (TDBBs) for health could be established using movement metrics quantified by the tags, potentially facilitating the work of veterinary staff in the future. Of the movement metrics trailed, the variance in body attitude (i.e., pitch and roll values), the number of

45° turns and VeDBA showed promise when differentiating between healthy and recovering turtles. However, the small sample sizes (and the limitations imposed by variation in turtle weight, GE severity and tank size), and the slow rate at which they can be increased (waiting for new cases etc.), makes this type of study particularly challenging. Nonetheless, this work is a start, and the results can be added to by other workers to give these findings credence, or not, as appropriate. Below, I consider how these data reflect my suppositions about GE-affected and healthy turtle behaviours before considering a holistic approach for helping define turtle condition from movement metrics. My analysis focused on metrics that revealed potential health dependent movement differences that could, in future, aid the creation of TDBBs.

4.1 Do patterns in surfacing behaviour reflect turtle health status?

Although there appeared to be a superficial difference in the 24-hour frequency of depth profiles between GE and healthy turtles (Figure 4), the considerable overlap in pressure variance between the two groups (across all the timeframes sampled) made it impossible to allocate individuals in a statistically meaningful way to either group. Thus, either my anecdotal observations are incorrect or possibly different depth-related movements over time, such as more frequent surfacings by GE animals, do not result in differences in time/depth allocations. This problem will only be exacerbated by poorly resolved depth data (Holton et al. 2021) and by shallow holding conditions so that will prevent periods of apnoea could not being definitively ascribed. In a similar manner, behavioural differences between healthy and convalescent turtles may also have been more apparent had I been able to mark discreet surfacing events confidently: tag placement on the carapace often resulted in tags not breaking the surface in unison with the head, especially if the turtle was swimming or floating close to the surface. As such, the use of pressure values to mark surfacing or breathing events for animals in shallow tanks, especially when tags are not attached to the head, is likely to be of limited accuracy. This approach may, however, be suitable for wild turtles that may dive tens to hundreds of meters deep and stay submerged for longer (Hochscheid 2014) thus making surfacing events more obvious. Furthermore, upon breaking the surface, exhaling and inhaling, wild turtles undergo changes in pitch angle that can be detected *via* motion and orientation-sensitive tags (Okuyama et al. 2014). Such clear changes in pitch could not be consistently identified in the shallow rescue centre tanks in order to mark surface or bottom intervals accurately.

Despite the failure of pressure variance as a metric, there may be a case for considering depth over longer intervals because I noted that pressure variance was most similar between the groups shortly after turtles had been admitted to a tank (in the 1.5 hours following a 1-hour acclimatization period). Similarities over this timeframe may have resulted from handling stress (Grandin 1997; Moberg 2000; Carere & Oers 2004; Waiblinger et al. 2004; Gourkow & Fraser 2006; Hemsworth et al. 2011), tag attachment (Bridger & Booth 2003; Geertsen et al. 2004; Vandenabeele et al. 2011; Walker et al. 2011; Thomson & Heithaus 2014) and being released into an unknown environment (Teixeira et al. 2007; Roe et al. 2010). In addition, convalescent turtle behaviour may have also been affected by medication (such as painkillers, sedatives), hyperbaric treatment and re-entering the water after many hours on land. A study to examine the potential for refining depth metrics could maintain tags on treated animals for extended periods to see how measured parameters change as the animals habituate to the veterinary procedures and their new environment. This, however, would substantially reduce the value of such metrics as a diagnostic since rapid time in diagnosis is advantageous.

4.2 Does activity measured using just VeDBA differ with turtle health status?

The idea that activity, as manifest by VeDBA, should differ between the two groups was founded on the belief that GE and healthy turtles had different resting/surfacing regimes (see section 4.1), so it was a little surprising that VeDBA values (averaged over 24 hours) showed no clear links with whether a turtle was healthy or convalescent or indeed with turtle mass. Similarly, 24-hour VeDBA frequency distributions showed substantial overlap between the two groups (Figure 7) even though 14 of 20 healthy turtles had a visually apparent pronounced decline towards an inflection point in the frequency decay while 6/20 healthy animals and all GE animals did not (see Appendix C, Figure C1). An attempt to formalize this using bent-cable models, reasoning that identification of an inflection point in 2D space could perhaps be definitive for healthy animals where it occurred, was disappointing because the descriptors for the change point, ‘α_cp’ and transition zone ‘γ’ overlapped substantially. Based on this part of the analysis, I believe that consideration of VeDBA distributions alone is inadequate to determine whether turtles are healthy or are suffering from GE; given the generic nature of DBA metrics and the confines of the turtles’ tanks (which will constrain movement greatly anyway) with hindsight this is hardly surprising. In addition, it is worth noting that, although animal activity and behaviour are commonly deduced *via* acceleration traces and wave patterns therein (*cf.* Brown et al. 2013; Wilmers et al. 2015), DBA metrics are relatively crude when used in isolation (Gunner et al. 2020). In the particular instance of turtles, DBA metrics are considered especially inappropriate since turtles move slowly, producing a poor dynamic signal (Gunner et al. 2020; Wilson et al. 2020a).

4.3 Do pitch and roll and VeDBA vary with turtle health status?

One of the first uses of accelerometers in biology demonstrated the value of using pitch to define behaviour in wild penguins (Yoda et al. 1999) and there have been many subsequent examples (Hochscheid et al. 1999; Shepard et al. 2008b; Wilson et al. 2008; Friedlaender et al. 2011; Brown et al. 2013; Wilson et al. 2016; Cox et al. 2018; Wilson et al. 2020a). In fact, presentation of the static acceleration, as a precursor to pitch and roll, was even shown to discriminate affective state in African elephants, *Loxodonta africana* (Wilson et al. 2014) so it seemed logical to examine whether GE-afflicted turtles had a change in body attitude (*cf.* Shepard et al. 2008b) compared to healthy animals. Hypothesis 3, that GE related injuries may impair manoeuvrability and lead to instability and greater variability in pitch and roll angles, appeared to be backed up by simple visual inspection of pitch and roll distributions (Figure 8a–d). In fact, this proved naive as variance values for pitch and roll in GE animals were generally well within the healthy turtle range. Against this however, plots of pitch or roll variance against VeDBA variance revealed rather, that healthy turtles tended to predominate in the area of the graphs characterised by higher variance of both parameters whereas GE-affected animals did not (Figure 9). This then, though contrary to my suppositions, would appear to be the beginning of a discriminatory process whereby any animal that showed high variance in pitch and/or roll coupled with high variance in VeDBA was statistically more likely to belong to the healthy turtle pool. Low variance in these parameters, however, did not give a significant probabilistic diagnosis for GE-affected animals since some healthy animals also inhabited this region.

Reasons for GE turtles not inhabiting the high pitch/roll and VeDBA variance sector may be that GE turtles do not display bursts of intense swimming activity to the same extent as healthy animals. Such bursts would tend to increase VeDBA and, because tank walls constrain proper movement, would also tend to produce more body pitch and roll extremes because the flippers strike the wall causing the carapace to rock. Both of these processes will increase the overall variance. Whatever the explanation, the 2D area of the pitch/roll variance *versus* VeDBA variance graph seems to be a useful indicator of healthy turtles.

4.4 Is turning behaviour indicative of health status?

Hypothesis 4, that GE-affected turtles would turn more, was generally supported by my findings because convalescent turtles usually performed a higher number of turns in the yaw axis per hour at each of the sampled turn thresholds (Figures 10 and 11). Curiously though, the relationship between the number of turns per hour and mean VeDBA was different for GE-affected and healthy animals (Figure 11), with healthy turtles having a higher VeDBA-specific turn rate. VeDBA is widely accepted as a good proxy for energy expenditure (Halsey et al. 2011b; Qasem et al. 2012) including for turtles (Enstipp et al. 2011; Halsey et al. 2011a) and turning imposes an energetic cost (Wilson et al. 2013; Crossley et al. 2018), which explains why turn rates increase with VeDBA. But it would also superficially appear that healthy turtles are less efficient at turning. This, however, assumes that a major part of VeDBA is consecrated to the turning process, which it clearly is not. Instead, I suggest that a higher proportion of VeDBA-manifest activity is involved in turning in GE-affected turtles than healthy animals. In other words, healthy animals display more activity that is not associated with turning although what these behaviours are, is unclear. Concomitantly though, healthy turtles had higher goodness-of-fit metrics than the GE turtles (Figure 11e), which indicates more consistent partitioning of VeDBA to turning and other (non-turning) activities and perhaps indicates that healthy behaviour is, in this sense, more predictable than the anomalous (García-Párraga et al. 2014), more erratic behaviour of the GE animals. The observations of these differences between GE-affected and healthy turtles in two-parameter plots indicates potential differentiation between groups on probabilistic grounds.

4.5 In search of a framework for defining animal condition based on movement metrics…

Four initial hypotheses were devised based on expected movement patterns, and although certain behavioural traits appeared to occur more frequently within the healthy or convalescent turtle group, high inter-individual overlap meant that none of the simple metrics tested in isolation revealed movement patterns that were consistently exclusive to either group. At face value, this may simply be because there are no state-specific differences in behaviour, but it may also be due to great inter-individual differences *per se*, even if there are real differences. To this can be added the complication of turtles being brought into rehabilitation, in some cases apparently healthy and in others subject to a suite of issues ranging from injuries to the carapace and flippers, internal and external infection and differing levels of GE (García-Párraga et al. 2014; Fahlman et al. 2017), each of these being manifest to a variable extent. All of this may affect movement patterns in ways that complement or go against patterns expected from the specific condition being considered (in this case GE) which will tend to blur boundaries and reduce the utility of descriptors. In short though, and from a practical perspective, the high variability observed in the simple metrics for state proposed here, would seem to preclude their utility for helping diagnose condition in individual animals.

However, a more sophisticated approach, which combines simple metrics, such as modelling the relationship between mean VeDBA and the number of 45º turns per hour did show significant differences between the healthy and GE groups, demonstrating the potential of tag-derived metrics and defining statistical confidences. These findings can become more potent if they can be combined, like in a dichotomous key or a disease/injury identification guide (see Appendix F), increasing the probability of correct diagnosis. Furthermore, combining tag-derived movement metrics (like VeDBA and/or turning) with body health indices (*cf.* Clegg et al. 2015; Shorter et al. 2017; Schiffmann et al. 2018) may also reveal useful links between behaviour and health.

Obvious limitations of this work were the small sample size, variable treatment conditions and animal size and sex, which are likely to decrease the value of the approach. For example, differences in tank size might be expected to affect behaviours like turning, especially in larger turtles, forcing them to turn more frequently upon reaching the side of the tank. Although this did not appear to be the case– no clear relationship between CCL and turning was found– in fact turtles with similar CCLs displayed vastly different turning rates, even when held in tanks of the same size. With several confounding factors at play, deducing which factors are influencing certain behaviours is challenging. These things can, however, be somewhat mitigated by increasing sample sizes, which could happen at a global level, rather than being dependent on just one institution such as Oceanogràfic.

I also note that my interrogation of movement metrics is not exhaustive and a suite of other possible variables such as waveforms within acceleration axes (Shepard et al. 2008b), from both static and dynamic acceleration (Qasem et al. 2012), and patterns within differential signals across sensors (e.g. Wilson et al. 2018a) could be considered. Inevitably though, as the number of potential descriptors increases, it becomes increasingly difficult to deconstruct them by hand. In this regard, computational solutions such as machine learning (Ladds et al. 2017; Brewster et al. 2018; Wang 2019), may become more prevalent. This may be particularly important as signals for behaviours become compressed or curtailed by small animal enclosures (Li et al. 2007; Leone & Estevez 2008; Ross et al. 2009; Neal Webb et al. 2018). In fact, animal enclosure size represents a major challenge to studies such as this one, not just because animals cannot engage in many natural behaviours (a good example here might be turtles diving to depth) but because preclusion or curtailment of behaviours means that long periods of uninterrupted signals are not available for analysis and because the limits of confinement force the animal to change behaviour anyway.

Despite these challenges, this study does demonstrate real potential for animal movement metrics derived from animal-attached tags in assessment of animal disease state, with indications that a similar approach might even be useful in identifying other issues such as animal welfare. The extent to which this happens though, will depend on engagement by captive animal exhibits, including rehabilitation centres, and personnel dedicated to the onerous process of systematic documentation of procedures. With the right impulse though, the future could see widespread adoption of animal-attached tags to the benefit of animals, from a suite of species, and their keepers alike.

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Chapter 4

Nutritional enrichment: using biologging to investigate whether motile or sessile prey types elicit different behavioural responses in sea turtles

Abstract

Environmental enrichment is a dynamic process, the aim of which is to enhance animal welfare by providing a greater variety of options that encourage a broader range of species-specific behaviours. The importance of enrichment has been advocated for large mammals to reduce abnormal or stereotypic behaviours such as pacing and head rolling but recently it has been demonstrated that reptiles also benefit from increased behavioural choices. Motion- and orientation-sensitive tags were attached to loggerhead turtles, *Caretta caretta,* in a controlled environment to measure behavioural responses during nutritional enrichment trials using sessile and motile prey (live clams and crabs, respectively), in contrast to their typical mixture of frozen squid, fish and vegetables in jelly. Turtle behaviour was examined using multiple movement metrics including overall activity (measured using dynamic body acceleration, DBA), changes in body pitch, roll and yaw, body angular velocity and the extent of turning. Contrary to what was expected, turtle behaviour only differed significantly with prey type for two of the selected metrics: heading variance and the rate of completion of 180º turns. The results presented here reveal that enrichment procedures may not always have expected or desired impacts on captive animal behaviour, highlighting the importance of collecting behavioural information in a quantifiable and robust manner. In future, data from multi-sensor tags could help zoos and aquariums create environments that elicit desired activity levels and behaviours, ensuring animal welfare by providing quantitative measures that can be used to assess well-being.

1. Introduction

Environmental enrichment (see Shyne (2006) for review) aims to enhance animal welfare by providing a greater variety of choice for confined animals to encourage a broader range of species-specific behaviours (Newberry 1995; Mellen & Sevenich MacPhee 2001; Buchanan-Smith 2010). Types of enrichment are generally divided into five categories; nutritional, structural, sensory, social and cognitive (Buchanan-Smith 2010) and there are numerous studies that have demonstrated the benefits of enrichment for animals maintained in controlled environments (see Shyne (2006) and references therein). In the past, the importance of enrichment has been emphasised for large mammal species, often with the goal of reducing abnormal or stereotypic behaviours such as pacing and head rolling (Mason & Latham 2004; Shyne 2006). Enrichment, for mammalian carnivores is often based on approaches linked to feeding, and has taken many forms including; the provision of live prey (Bashaw et al. 2003), intact carcasses (Veninga & Lemon 2001; McPhee 2002), artificial prey (Markowitz et al. 1995), odours/scent (Williams et al. 1999; Cohen & Moore 2001), food puzzles (Lyons et al. 1997; Jenny & Schmid 2002) and physical toys (Knowles & Plowman 2001).

More recently, it has been demonstrated that reptiles benefit from increased behavioural choices in a manner similar to mammals (Almli & Burghardt 2006; Manrod et al. 2008; Noble et al. 2012; Bashaw et al. 2016; Benn et al. 2019). Zoos and aquariums regularly achieve this through cognitive research and training, enabling animals to make choices and gain some control over their environment (Alba et al. 2017). For example, the Conservation Station at Disney's Animal Kingdom® has carried out cognitive research sessions with Eastern box turtles (*Terrapene carolina carolina*) for the past several years (Leighty 2012; Leighty et al. 2013; Alba et al. 2017). In one particular experiment, these animals spent less time resting and more time trying to escape in a barren environment than an enriched one (Case et al. 2005). Studies like these demonstrate the need for effective enrichment strategies that go some way to meeting the behavioural needs of a species (Bacon 2018).

Animal welfare is a high priority for zoos, aquaria, and pet owners alike (Bashaw et al. 2016). Animal welfare assessment methods in the past have often focused on resource-based measures, recorded in the animals' environments, and include elements like space, lighting and food requirements, all of which are easily quantifiable and repeatable for individuals and groups (Benn et al. 2019). These measures, however, may not reflect the condition or affective state (Benn et al. 2019) of an animal, which is why welfare assessments have shifted towards using animal-based indicators, combining behavioural, physiological, and health-related variables (Whitham & Wielebnowski 2013; Mellor & Beausoleil 2015). The affective state of an animal can be described as positive, (i.e., expressed as 'happiness' in humans) or negative (involving feelings such as fear, depression and pain), and the balance of these states over time can be used to infer well-being (Boissy et al. 2007). Animal-based indicators are generally considered more comprehensive measures of welfare (requiring an understanding of the animal and its interactions with its environment), but their implementation can be problematic because recording variables is time-sensitive and they have limited repeatability due to subjectivity (Bashaw et al. 2016; Blatchford 2017). As a result, current reptilian welfare assessments still usually focus on resource-based measures (Benn et al. 2019).

Given that reptiles are frequently housed in zoos and aquaria and are increasingly kept as pets, the lack of welfare assessment methods (compared to mammals) and the tendency to rely on resource-based measures needs addressing (Bashaw et al. 2016; Benn et al. 2019). In some cases, appropriate animal-based indicators may be created by modifying existing welfare assessment tools. For example, Benn et al. (2019) used the Welfare Quality® Protocol (designed for farm animals) to define suitable animal-based indicators for the pygmy blue-tongue skink (*Tiliqua adelaidensis*). The study focused on indicators that would reflect good feeding (i.e., the absence of hunger and thirst), good health (i.e., the absence of injury or disease), and good housing (indicated by appropriate time spent basking, shedding, and panting). In another study, Leopard geckos (*Eublepharis mascularius*) that were exposed to the five different types of enrichment (nutritional, structural, sensory, social and cognitive (Buchanan-Smith 2010)) predominantly responded to nutritional and sensory (thermal) enrichment– potentially because this best met their behavioural requirements (Bashaw et al. 2016).

Positive welfare states are encouraged by meeting an individual's essential needs (thus minimising survival-related negative effects) and by creating a stimulus-rich environment in order to replace situation-related negative effects with positive stimuli (Mellor & Beausoleil 2015). In comparison to negative affective states, positive ones, such as play, are under-researched, particularly in reptiles because they are difficult to define; this avenue of research deserves more attention because maintaining a positive affective state is a tenet of good animal welfare (Boissy et al. 2007; Mellor 2012).

Although play (defined as behaviour that is spontaneous, pleasurable, and not fully functional (Burghardt 2005)) is less often associated with ectothermic species (in part due to unnecessary metabolic costs), studies have shown that reptiles are capable of play and can even benefit from problem-solving activities (Burghardt 1990, Burghardt 2005). In one study, the provision of balls, sticks and hoses (structural enrichment) to a Nile soft-shelled turtle (*Trionyx triunguis*) maintained in a zoo, both increased its activity levels and greatly decreased its self-mutilation behaviour, indicating that play is of benefit to captive reptiles which do not have the metabolic costs of wild ones (Burghardt et al. 1996). Other studies have also used the scent of prey (sensory enrichment) within objects placed within a reptile's enclosure as a form of enrichment (Burghardt 1990). Reptilian play behaviour has been more frequently reported in the larger, long-lived species such as monitors and turtles (Burghardt 2005), indicating that for these groups, play may be a valuable welfare indicator (Benn et al. 2019).

As comprehensive measures of welfare, the incorporation of animal-based indicators into welfare assessments is considered important (Benn et al. 2019) and would be greatly facilitated by recording and quantifying animal movement in a non-subjective and timely manner (Arkwright et al. 2020). Advancements in logger technology have been fundamental in improving our knowledge of wild animal movement ecology (Ropert-Coudert & Wilson 2005; Nathan et al. 2008; Wilmers et al. 2015) and behaviour (Naito 2004; Whitney et al. 2010; Brown et al. 2013; Whitney et al. 2016), and given this, multi-sensor tags may prove a valuable tool for studying the effects of enrichment, animal well-being, and for welfare assessments.

To explore this concept, motion- and orientation-sensitive tags (Shepard et al. 2008b; Wilson et al. 2008) were attached to loggerhead sea turtles (*Caretta caretta*) and used to examine their behaviour during nutritional enrichment trials with moving and stationary prey types. The objective was to assess whether detectable changes in animal movement, and therefore behaviour, were associated with feeding and the different prey types: behaviour and movement are intrinsically linked (Shepard et al. 2008b; Nathan et al. 2012; Williams et al. 2017) because animal behaviour is typically defined by movement (Tinbergen & Iersel 1947; Tinbergen 1952, 1959). Working on the premise that biologging has already been used to provide metrics on animal state (Wilson et al. 2014), tags were deployed to investigate whether different prey types elicited different behavioural responses manifest *via* movement metrics. Specifically, I was interested in investigating whether:

i. *Acceleration-based activity or proxies for energy expenditure* varied during and after feeding trials according to food type.
ii. *Pitch, heading and roll metrics*, i.e., rotational movement about the lateral, longitudinal or vertical axes, respectively, changed during and after feeding with live food.
iii. *Angular movement* assessed *via* angular velocity, absolute angular velocity (AAV; see section 2.8) and the total number of 45° and 180° turns per unit time interval increased during and after feeding.

In all cases, it was hypothesised that the stationary prey would elicit less of a response than the motile prey during the feeding trial and for the following few hours.

2. Method

2.1 Feeding trials

In summer 2018, feeding trials took place with loggerhead turtles in the Arca del Mar rehabilitation centre (Valencia, Spain) in rescue centre tanks (2–6 m in diameter and 0.95 m deep). During the trials, the turtles were fed three types of live prey: moon jellyfish (*Aurelia aurita*), clams (either Japanese clams, *Ruditapes phillipinarum* or Venus clams, *Chamelea gallina*) and green shore crabs (*Carcinus maenas*). The moon jellyfish were substituted for clams after six trials because turtles displayed little interest in them, leaving a number of jellyfish uneaten.

The feeding experiments were carried out with nine different study animals (see Table 1) and often the same individual took part in multiple feeding sessions, resulting in a total of 31 trials. All trials were video recorded using a GoPro HERO4 in order to timestamp feeding events for comparison with the tag data and to record the approach time (defined as the number of seconds between the moment the turtle started swimming toward the prey and the first successful bite). Turtles were tagged opportunistically.

To ensure that the turtles were sufficiently hungry, the experiments were performed before animals received their usual food and only on Mondays and Thursdays (as turtles were not fed on Wednesdays and weekends); the same turtle never took part in more than two feeding trials in any one week. Normally, turtles were fed a mixture of squid, fish (such as mackerel and sardines) and vegetables (such as carrots, zucchini and spinach) held together in jelly with nutrients and vitamins added at veterinary discretion.

Before each feeding trial, the motion-sensitive tags (see section 2.3) were attached to each turtle’s carapace with the animal out of the water (see section 2.2). Once reintroduced into their tank, individuals were given 15 minutes to acclimatise before the first food item was given (the acclimatisation period was necessarily short in order to have finished the feeding trials in time for normal feeding). Each feeding trial lasted 25 minutes and prey items were released every five minutes, resulting in five items being given per experiment (initially only three prey items were given per trial as turtles displayed little interest in the jellyfish, the number was increased to five after turtles showed increased interest in crabs). The trial duration and the intervals at which the prey was given were kept the same, regardless of whether the turtle ate or not. Any uneaten food items were removed from the tank shortly after the experiment.

When possible, tags were left attached in order to collect ‘post-trial’ data as well as ‘during-trial’ data; this ‘during- and post-trial’ data was collected over a 250-minute period beginning with the 25-minute feeding trial (the 250 minutes facilitated data being sampled at 25-minute intervals, yielding ten data points). All experiments were approved by the Animal Care and Welfare Committee (OCE-16-18) at the aquarium.

Table 1. Summary of tagged turtles including turtle identification number, entry to and release dates from the rehabilitation centre, bycatch origin, curved carapace length CCL (cm; turtle weight (kg) is provided in Appendix G), cause of injury/disease (when known), the turtles' state of health upon entry and the dates of the turtles' first trials (also the first date of tagging). All animals were 'healthy' when tagged. State of health was deduced following veterinary examination; gas emboli (GE) was categorised according to methods described in García-Párraga et al. (2014) and Fahlman et al. (2017).

Turtle ID	**Entry**	**Release**	**Origin**	CCL (cm)	**Cause of injury/ disease**	**State of health upon entry**	**Date of first trial**
T348	21/11/2017	13/07/2018	Vinaroz	34	Trawl/ bottom fishing	Mild GE	28/06/2018
T385	18/03/2018	20/07/2018	Valencia	40.7	Trawl/ bottom fishing	Healthy	21/06/2018
T396	28/03/2018	05/07/2018	Vinaroz	59	Trawl/ bottom fishing	Healthy	28/06/2018
T397	05/04/2018	03/06/2018	Gandia	39	Trammel net	Drowned and resuscitated	30/05/2018
T399	06/04/2018	08/06/2018	Cullera	40	Trammel net	Healthy	30/05/2018
T402	16/04/2018	09/06/2018	Burriana	36	Trawl/ bottom fishing	Healthy	30/05/2018
T403	06/05/2018	29/06/2018	El Perello	38	Unknown (found floating at surface)	Healthy	11/06/2018
T404	07/05/2018	06/07/2018	Almenara	30	Unknown (found floating at surface)	Wounded neck	11/06/2018
T405	01/06/2018	12/07/2018	Peniscola	64	Trawl/ bottom fishing	Very mild GE	28/06/2018

2.2 Tag attachment

To attach the motion-sensitive tags, bycaught turtles were lifted out of their holding tank and placed onto a foam mat inside a plastic box. Tags were attached to the second central scute of the carapace with a two-part epoxy (Veneziani Subcoat S, https://www.venezianiyachting.com/en/products/fillers), pre-mixed in water. The turtle was left in the box for approximately 10 minutes whilst the epoxy dried. The devices weighed between 25–40 g and were approximately 60 x 40 x 19 mm, (size varied by ± 10 x 10 x 6 mm).

2.3 Data collection and analysis

The motion sensitive tags were Daily Diaries (DDs; http://www.wildbytetechnologies.com /tags.html) and logged tri-axial acceleration, tri-axial magnetic field strength, ambient temperature, and pressure at 20 Hz per channel (Wilson et al. 2008). Acceleration was recorded in *g* (range; ± 16 *g*) and magnetometry was recorded in Gauss (G) with 0.73 mG/LSb resolution (range ± 0.88 G). Both acceleration and magnetic field strength were recorded along three orthogonal axes which correspond to the dorso-ventral, lateral, and anterior-posterior axes of the animal (Williams et al. 2017). For accelerometry data, these correspond to the heave, surge and sway axes (x, y and z axes), respectively. The magnetometry data, in tandem with the acceleration data, provide information on the animal's angular rotation; pitch, roll and yaw (Williams et al. 2017; Gunner et al. 2021).

Tag data were initially visualized using 'Daily Diary Multi Trace' (DDMT; open source, http://www.wildbyte-technologies.com), a custom-designed software that displays accelerometry, magnetometry, pressure and temperature channels on the y-axis and time on the x-axis. The software also calculates and displays useful derivatives from raw data, such as the vector of the dynamic body acceleration, VeDBA (Qasem et al. 2012), a powerful proxy for energy expenditure (*cf*. Halsey et al. 2011a; Halsey et al. 2011b; Wilson et al. 2020a), and the differential (i.e., rate change) of any desired channel. It also runs smoothing windows of various lengths through a specified channel, as well as facilitating the search for specific behaviours *via* the creation of Boolean-type, time-based behavioural expressions (Wilson et al. 2018a).

2.4 Movement metrics used

The computation of selected movement metrics; VeDBA, pitch, heading, roll, AAV and turn extents of 45º and 180º, is detailed in sections 2.4.1–2.4.4 (in line with aims i., ii. and iii.). These metrics were smoothed over two seconds in DDMT to reduce noise and were then subsampled at 1 Hz in RStudio (version 3.6.0, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/) for further analysis. This was done to facilitate analysis and was without analytical consequence because turtles are typically slow-moving with VeDBAs usually below 0.08 *g* (Gunner et al. 2020).

2.4.1 Calculating components of acceleration

The ‘static’ component of acceleration due to gravity (which amounts to 1 *g* or 9.81 ms^{-2}) was computed by using a moving average of a given window size (*w*) through a given sample (S_i) of each of the orthogonal acceleration channels (Fang et al. 2005). Based on recommendations in Shepard et al. (2008a), a two second window was implemented.

$$S_i = \frac{1}{w} \sum_{j=i-\frac{w}{2}}^{i+\frac{w}{2}} S_j$$

The ‘static’ acceleration of each axis was subtracted from the raw acceleration of each axis, leaving the ‘dynamic’ component of acceleration (Bidder et al. 2015; Gunner et al. 2020). The vectorial dynamic acceleration (VeDBA (*g*)), a proxy for energy expenditure (Wilson et al. 2020a), was then calculated using the vectorial sum of dynamic acceleration (*DA*) of the three orthogonal axes *x, y* and *z*, squared (Qasem et al. 2012) according to;

$$VeDBA = \sqrt{DA_x^2 + DA_y^2 + DA_z^2}$$

2.4.2 Calculating pitch and roll

Pitch and roll (°) were computed using the static acceleration of the *x*, *y*, and *z* channels, denoted S_x, S_y and S_z, corresponding to the heave, surge, and sway axes respectively (Bidder et al. 2015).

The *'atan2'* function computes the angle between two coordinates given as arguments, separated by a comma, and can be found in Matlab and Microsoft Excel (Bidder et al. 2015).

$$Pitch = \left(atan2\left(S_x, \sqrt{S_y \bullet S_y + S_z \bullet S_z}\right)\right) \bullet \frac{180}{\pi}$$

$$Roll = \left(atan2\left(S_y, \sqrt{S_x \bullet S_x + S_z \bullet S_z}\right)\right) \bullet \frac{180}{\pi}$$

$$atan2(y, x) = 2\, arctan \frac{y}{\sqrt{x^2 + y^2} + x}$$

2.4.3 Calculating animal compass heading

First, deformations and offsets in magnetic field data were corrected in DDMT using calibration data which was created by rotating the DD tag so that all orientations of roll, pitch, and yaw were covered (Williams et al. 2017). The calibration data forms a sphere when plotted as a tri-axial magnetic field intensity scatterplot, giving a frame of reference for the tri-axial magnetometry data (Williams et al. 2017). This frame of reference was then used to compensate 'hard' and 'soft-iron' distortions in the local magnetic field (Gunner et al. 2020): whilst the former shifts the magnetic field and hence the sphere away from its origin, the latter deforms the magnetic field about the sensor, turning the sphere into an ellipsoid (Gebre-Egziabher et al. 2006; Ozyagcilar 2012). An ellipsoid-fitting algorithm with a correction factor were used to return spherical fields to their true origins and correct deformations in shape (Bidder et al. 2015; Walker et al. 2015).

Angular rotations across pitch and roll axes were used in the tilt correction procedure on each orthogonal magnetometer channel (Bidder et al. 2015). Compass data were normalised before each orthogonal channel was rotated according to pitch and roll, ensuring that the magnetometry channels were compensated, accounting for changes in angle resulting from postural offsets, with values corrected to give a horizontal co-ordinate frame (Bidder et al. 2015).

Animal compass heading (*H*) ranging from 0–360°, with both 0° and 360° equating to Magnetic North (Gunner et al. 2020), could then be computed (see following page). Note: *mod* is the modulo operator and m_y and m_x are the normalized, ellipse-fitted and co-ordinate frame-adjusted *x* and *y* channels of the magnetometer respectively (Bidder et al. 2015; Gunner et al. 2020).

$$H = mod\left(360 + \left(atan2(-m_y, m_x) \bullet \frac{180}{\pi}\right), 360\right)$$

Heading was then converted from degrees to Cartesian coordinates to bypass problems when calculating the arithmetic mean that are caused by heading data being cyclical, i.e., both 0° and 360° define the Magnetic North on a circle (Pewsey et al. 2013). The arithmetic mean of individual angles ($\hat{\theta}$) was then computed from sample trigonometric moments and the resultant units restored back to degrees ($\widehat{H}$).

$$\hat{\theta} = atan2\left(\frac{1}{n}\sum_{j=i}^{n} sin\left(H_j \bullet \frac{\pi}{180}\right), \frac{1}{n}\sum_{j=i}^{n} cos\left(H_j \bullet \frac{\pi}{180}\right)\right)$$

$$\widehat{H} = mod\left(360 + \left(\hat{\theta} \bullet \frac{180}{\pi}\right), 360\right)$$

Greater detail regarding the computation of pitch, roll and compass heading is available in Walker et al. (2015), Bidder et al. (2015) and Gunner et al. (2020).

2.4.4 Computing absolute angular velocity

The absolute angular velocity, AAV(°/s), is derived from the integration of pitch, roll and yaw axes to provide absolute instantaneous angular velocity of the body trunk in 3-dimensional space (Gunner et al. 2020). Differential angular velocities about the pitch, roll and yaw axes, denoted: '*DAVP'*, '*DAVR'* and '*DAVY'*, respectively, were created in DDMT after the two second smoothing window had been passed through the values of each axis, using a stepping range of one second (Gunner et al. 2020).

$DAVY = x_{j+1} - x_j$

$DAVP = x_{j+1} - x_j$

$DAVR = x_{j+1} - x_j$

where x is the *ith* value of yaw, pitch or roll (Gunner et al. 2020). The absolute angular velocity (per second) is then given by:

$$AAV = \sqrt{(DAVY^2 + DAVP^2 + DAVR^2)}$$

Given that heading is circular with no true zero, assigned high and low values were arbitrary. A logical expression for the *DAVY* prevented the rate of change surpassing 180°/s, otherwise it is not clear whether the animal has turned towards the left or the right (Gunner et al. 2020). The turning ability of the study animal needs to be considered for the sampling interval of *DAVY*. Importantly, the interval must be shorter than the time taken to turn 180° in order for rate change calculations to be accurate (Gunner et al. 2020). Thus, the greatest achievable angle for any given axis per second was 180°.

The *DAVY* was used to measure when an animal completed a 45° and 180° turn. Angle extent was measured in RStudio using conditional running cumulative sum functions which reset to the starting orientation each time the selected angle threshold was attained.

2.5 Statistical analysis

Generalized linear mixed-effects models (GLMMs) were performed to analyse the behaviour of turtles in response to being fed five sessile or five motile prey items. I investigated whether either prey type (included as an explanatory variable), elicited a significantly different behavioural response in terms of approach time and for a variety of movement metrics (fixed effect continuous covariates) including activity (i.e., mean VeDBA and variance in VeDBA) and various types of rotational movement (including the variance in pitch, heading and roll, the mean and the variance in angular velocity and AAV, and the total number of turns reaching angle extents of 45º and 180º). A GLMM was conducted for each movement metric in order to avoid multicollinearity of incorporating similar movement metrics into the same model (Pitt & Myung 2002). Variable means for pitch and roll were not investigated due to minor offsets in their baseline values resulting from inter-individual differences in size, carapace slope and sensor inclination (Gunner et al. 2020): it was not possible to correct for these because turtles did not remain motionless in defined orientations post-tagging, as such, all analysis was performed with the variance (rather than the mean) of both variables.

GLMMs modelling approach time incorporated data from 47 clam feeding events (n = 12 trials) and 50 crab feeding events (n = 13 trials). GLMMs modelling behavioural responses *via* various movement metrics incorporated both 'during-trial' and 'during- and post-trial' data: for the latter, metrics were sampled at 25-minute intervals until ten data points had been reached, giving 250 minutes of movement data in total. As such, GLMMs combined 'during-trial' data from eight trials with clams and four trials with crabs, and 'during- and post-trial' data from four trials with clams and nine trials with crabs (where DDs had been left attached to collect data spanning the 250-minute period). Turtle ID was incorporated into each GLMM as a random effect to account for inter-individual differences such as turtle weight and sex (this would have led to overfitting if the GLMMs had not included post-trial data as well as data collected during trials).

The GLMMs were performed using the 'glmer' function from the 'lme4' package in R (Bates et al. 2014) and were fitted using a Gaussian, gamma or Poisson family (the variance function) with either a log or an identity link (a transformation of the mean of 'y'), in accordance with what best suited each variable's distribution. To interpret GLMMs with a log link, statistically significant coefficient estimates, and their standard errors were exponentiated. The best fitting model, (i.e., whether the 'null' or 'full' model) was determined through diagnostic plots and Akaike Information Criterion (AIC). The 'summary' function was used to extract *p*-values, thus giving a measure of significance for the coefficient estimates. All graphical representation was carried out using the 'ggplot2' package in R (Wickham 2016).

3. Results

Data from nine juvenile turtles (30–64 cm CCL) were included in this study (see Table 1). Feeding trials were performed with jellyfish (n = 6), crabs (n = 13) and clams (n = 12; Table 2) but jellyfish trials were not included in further analysis due to lack of response by the turtles and because three (instead of five) prey items were given, resulting in trials being shorter than the standard 25 minutes. In most of the clam and crab trials, the turtles ate the prey relatively quickly (within 2–3 minutes), a few turtles showed no interest in the prey (especially during jellyfish trials) and two turtles (T402 and T385) showed agitated and avoidance behaviour, swimming almost continually during the experiment. For feeding trials with clams and crabs, the mean approach time of the former was almost half that of the latter (96.78 s ± 171.70 SD and 175.22 s ± 334.52 SD, respectively). The large variation in approach time, however, resulted in no obvious differences in turtle responses to clam and crab prey types (Figure 1). A GLMM with Gaussian errors and a log link function also revealed that approach time did not differ significantly (i.e., $p < 0.05$) depending on prey type (Est. = 0.44 ± 0.32 (S.E), $t = 1.38$, $p = 0.17$; see Table 3, GLMM 1).

3.1 Activity

Turtle activity during the 25-minute feeding trials (Figure 2a, c) and over the 250-minute data collection period (Figure 2b, d) did not appear to differ in response to being fed either crab or clam prey types. Although the highest individual mean VeDBAs were recorded during and after crab trials (Figure 2a, b), combined mean VeDBAs were marginally lower than those observed during and after clam trials. Statistical analysis using the data collected during and post-trial revealed no significant (threshold $p < 0.05$) differences in mean VeDBA or variance in VeDBA depending on prey type (Table 3, GLMMs 2 and 3 respectively).

Table 2. Summary of feeding enrichment experiments: the tank size (given as the available water volume in L) and the number of prey eaten of the total given per trial are presented for all jellyfish, crab and clam feeding trials. Most turtles took part in several food trials. The result of each trial (the number of food items eaten), is separated by a semicolon. Trials conducted with the same turtle but in tanks of differing water masses are on separate lines while trials conducted in tanks with the same water mass are shown on the same line. Trials with jellyfish were discontinued due to a lack of response by the turtles and not included in analysis.

Turtle ID	**Jellyfish trials**		**Clam trials**		**Crab trials**	
	Tank size (L)	**No. eaten**	**Tank size (L)**	**No. eaten**	**Tank size (L)**	**No. eaten**
T348	-	-	7000	5/5; 4/5	7000	4/5; 5/5; 4/5
T385	-	-	3500 7000	3/5 5/5; 3/5; 5/5	7000	2/5; 1/5
T396	-	-	12000	4/5	12000	4/5; 5/5
T397	3500 7000	1/5 0/3	-	-	-	-
T399	3500	2/3	-	-	-	-
T402	1500	0/3	-	-	-	-
T403	3000	0/3	7000	2/5; 4/5	7000	5/5; 5/5
T404	3000	0/3	3000 7000	2/5 5/5	3000 7000	4/5 5/5
T405	-	-	19000	5/5	19000	4/5; 5/5

Table 3. Generalised linear mixed-effects models (GLMMs) for relationships between food and activity, with each family and link function specified. Models tested whether feeding trials with either clams or crabs elicited different behavioural responses in turtles. The AIC values were similar between each pair of null and full model, indicating minor differences in the goodness of model fit. All GLMM intercepts were highly significant, indicating that values were significantly different to zero. However, the effect of prey type on the various movement metrics tested was non-significant ($p > 0.05$) for all metrics apart from heading variance and 180º turns (GLMMs 5 and 12; significance indicated by asterisks, '' 0.01; '**' 0.001). Instead of t-values, z-values are presented for GLMMs 11 and 12 with Poisson error terms.*

GLMM	**AIC**	**Family**	**Link**	**Variable**	**Est.**	**S.E.**	***t*-value**	***p*-value**
Null 1	363.35	Gaussian	Log	Intercept	3.64	0.31	11.83	<0.0001
Full 1	363.52			Intercept	3.41	0.36	9.47	<0.0001
				Approach time	0.44	0.32	1.38	0.171
Null 2	-791.81	Gaussian	Log	Intercept	-3.07	0.04	-82.97	<0.0001
Full 2	-790.01			Intercept	-3.05	0.06	-55.22	<0.0001
				Mean VeDBA	-0.03	0.06	-0.45	0.652
Null 3	-1864.3	Gamma	Log	Intercept	-7.41	0.1	-73.7	<0.0001
Full 3	-1862.8			Intercept	-7.47	0.13	-56.27	<0.0001
				VeDBA variance	0.08	0.11	0.7	0.484
Null 4	1689.8	Gamma	Log	Intercept	5.06	0.09	56.82	<0.0001
Full 4	1691.5			Intercept	5.11	0.13	39.98	<0.0001
				Pitch variance	-0.07	0.12	-0.61	0.545
Null 5	2713.8	Gaussian	Log	Intercept	8.42	0.18	47.38	<0.0001
Full 5	2710.5			Intercept	8.55	0.18	46.65	<0.0001
				Heading variance	-0.18	0.07	-2.4	0.0162*
Null 6	1588.8	Gamma	Log	Intercept	4.75	0.26	18.55	<0.0001
Full 6	1590.8			Intercept	4.78	0.28	17.31	<0.0001
				Roll variance	-0.03	0.136	-0.22	0.828
Null 7	845.64	Gaussian	Identity	Intercept	8.77	0.46	18.87	<0.0001
Full 7	846			Intercept	9.51	0.74	12.81	<0.0001
				Mean angular velocity	-1.07	0.84	-1.28	0.203

Null 8	1690.5	Gaussian	Identity	Intercept	167.84	9.17	18.31	<0.0001
Full 8	1688.9			Intercept	189.03	14.4	13.1	<0.0001
				Angular velocity variance	-31.07	16.25	-1.91	0.0581
Null 9	739.83	Gaussian	Identity	Intercept	6.23	0.39	16.14	<0.0001
Full 9	739.99			Intercept	6.77	0.56	12.15	<0.0001
				Mean AAV	-0.77	0.58	-1.34	0.182
Null 10	1313.4	Gaussian	Identity	Intercept	54.74	2.41	22.71	<0.0001
Full 10	1312.1			Intercept	60.14	3.52	17.1	<0.0001
				AAV variance	-7.74	4.27	-1.81	0.0727
Null 11	5937.2	Poisson	Log	Intercept	4.62	0.05	101.7	<0.0001
Full 11	5938.8			Intercept	4.61	0.05	97.55	<0.0001
				45 turns	0.01	0.02	0.68	0.497
Null 12	2061.5	Poisson	Log	Intercept	2.96	0.1	28.52	<0.0001
Full 12	2054.4			Intercept	3.05	0.11	28.22	<0.0001
				180 turns	-0.13	0.04	-3.04	0.0024**

Continued.

3.2 Pitch, heading and roll

Rotational movement along the pitch, heading and roll axes both during- and post-trial did not appear to differ with prey type (Figure 3) despite some crab trial results having significant outliers (Figure 3b, c, d). The combined mean variance (indicated by larger solid circles in Figure 3) during and after crab trials appeared slightly lower for pitch and heading channels both during- and after feeding trials (Figure 3a, b, c, d). However only the variance in heading was found to differ significantly with prey type, with a significantly lower variance in heading being associated with crab trials, i.e., heading variance was 0.84 ± 1.07 times as high in trials with crabs (Est. = -0.18 ± 0.07 (S.E), t = -2.4, p = 0.02; see Table 3, GLMM 5). Differences in the variance in pitch and roll associated with clam or crab prey types were not significant (Table 3, GLMMs 4 and 6, respectively).

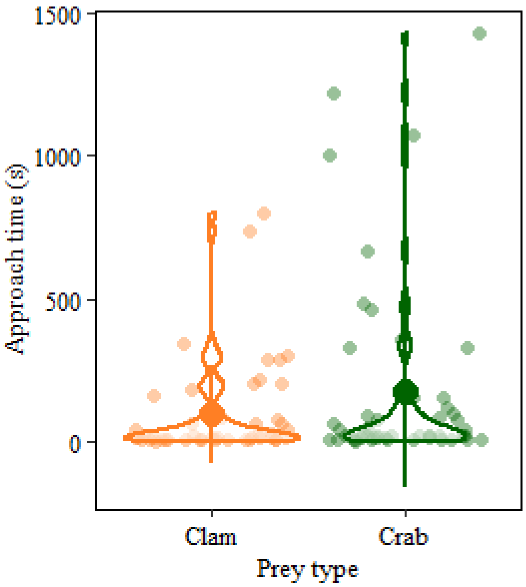

Figure 1. Violin plots of approach time in seconds for turtles in rescue centre tanks being fed clams (depicted in orange), and crabs (depicted in green) during 25-minute-long feeding trials; five prey items were given per trial, one every five minutes. The approach times (calculated from the moment the turtle began moving in the direction of the prey to the first successful bite) are given for 47 clam feeding events (n = 12 trials) and 50 crab feeding events (n = 13 trials). The outline of the violin plot indicates point density and the central circle and line indicate the mean ± SD respectively. Plots show no marked differences in approach time between prey types, and this was confirmed by statistical analysis (Table 3, GLMM 1).

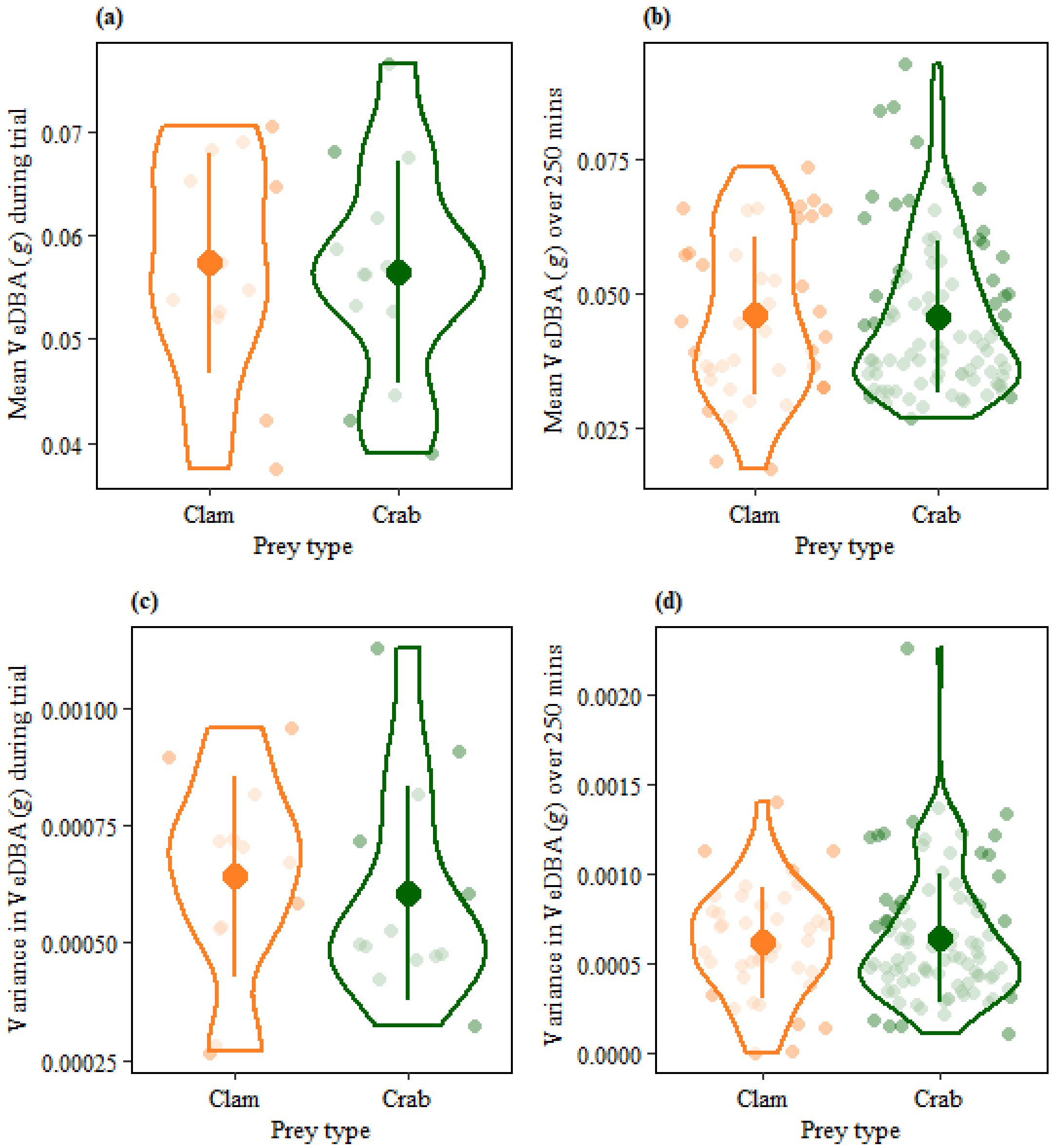

Figure 2. Activity data for turtles in rescue centre tanks during feeding trials with clams (depicted in orange), and crabs (depicted in green). Violin plots show (a) mean VeDBA and (b) variance in VeDBA during each 25-minute feeding trial, and (c) mean VeDBA and (d) variance in VeDBA over a 250-minute period (starting with a 25-minute feeding trial and continuing for nearly four hours thereafter). During trial periods, plots (a, c) present data from 12 trials with clams and 13 trials with crabs during and post-trial while plots (b, d) present data from four trials with clams and nine trials with crabs (each data point representing 25 minutes of data). The outline of the violin plot indicates point density and the central circle and line indicate the mean ± SD respectively. Plots show no marked differences in VeDBA between the prey types, and this was confirmed by statistical analysis (Table 3, GLMMs 2 and 3).

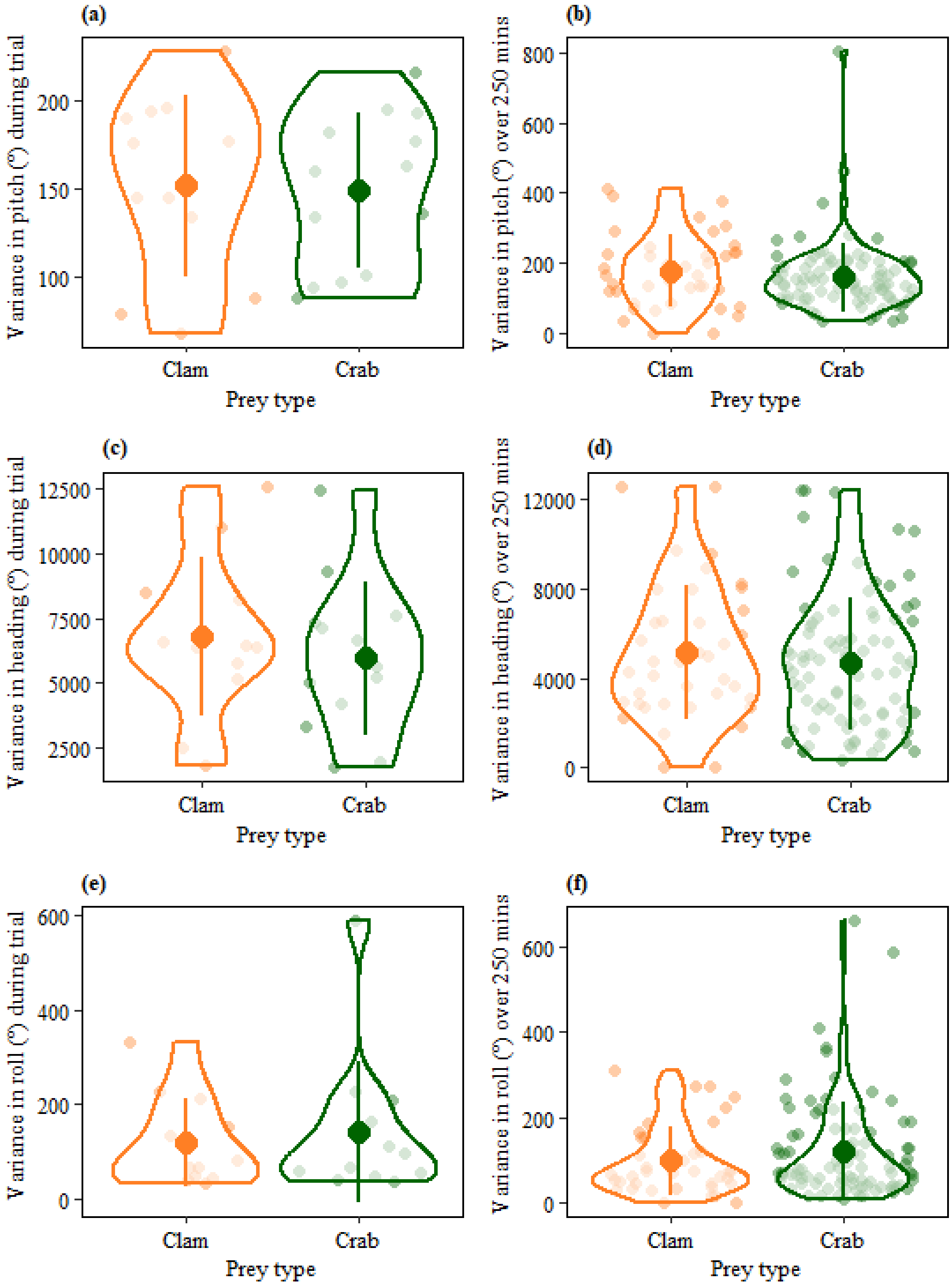

Figure 3. Movement data for turtles in rescue centre tanks during feeding trials with clams (depicted in orange), and crabs (depicted in green). Violin plots show (a, c, e) variance in pitch, heading and roll, respectively, during each 25-minute feeding trial, and (b, d, f) variance in pitch, heading and roll, respectively, over a 250-minute period (starting with a 25-minute feeding trial and continuing for nearly

four hours after). During trial data, plots (a, c, e) present data from 12 trials with clams and 13 trials with crabs; during and post-trial, plots (b, d, f) present data from four trials with clams and nine trials with crabs (each data point representing 25 minutes of data). The outline of the violin plot indicates point density and the central circle and line indicate the mean ± SD respectively. Although plots show no clear differences in rotational movement along the x, y, or z axes related to being fed clam or crab prey types, the variance in heading was significantly lower for trials with crabs (Table 3, GLMM 5); crab trials in plots (b, c, d) are skewed one or two outliers.

3.3 Angular velocity and turning

Rotational movement measured using angular velocity for all rotation axes combined (AAV– Figure 4) indicated no obvious differences in turtle behaviour relating to prey type: both the mean and the variance in angular velocity covered a wider range (especially towards upper extremes) in ‘during crab trial’ data (Figure 4a, c, respectively) although this pattern was less evident in data spanning a 250-minute period (Figure 4b, d). Similarly, data collected during crab trials also covered a wider spread than clam trial data in terms of mean AAV and variance in AAV (Figure 5a, c respectively) although the data from the majority of turtles was clustered. By contrast, AAV post-trial clam data appeared slightly more dispersed than crab data, though differences were not obvious (Figure 5b, d respectively). Statistical analysis using the data collected during and post-trial however, revealed no significant differences in either the mean or variance in angular velocity or the mean or variance in AAV (Table 3, GLMMs 7 and 8, *and* 9 and 10, respectively).

Turn rates per 25 minutes were similar between both prey type groups at both 45° and 180° angle thresholds (Figure 6). Discrepancies in the spread of data were due to individuals that completed very few or comparatively high numbers of turns (Figure 6a, c, d). Although there was no significant difference in the number of 45° turns (Table 3, GLMM 11) completed during and after trials associated with moving and stationary prey, the number of 180° was found to be significantly lower in trials with crabs: the number was 0.89 ± 1.04 times as high in trials with crabs (Est. = -0.13 ± 0.04 (S.E), t = -3.04, p = 0.002; see Table 3, GLMM 12).

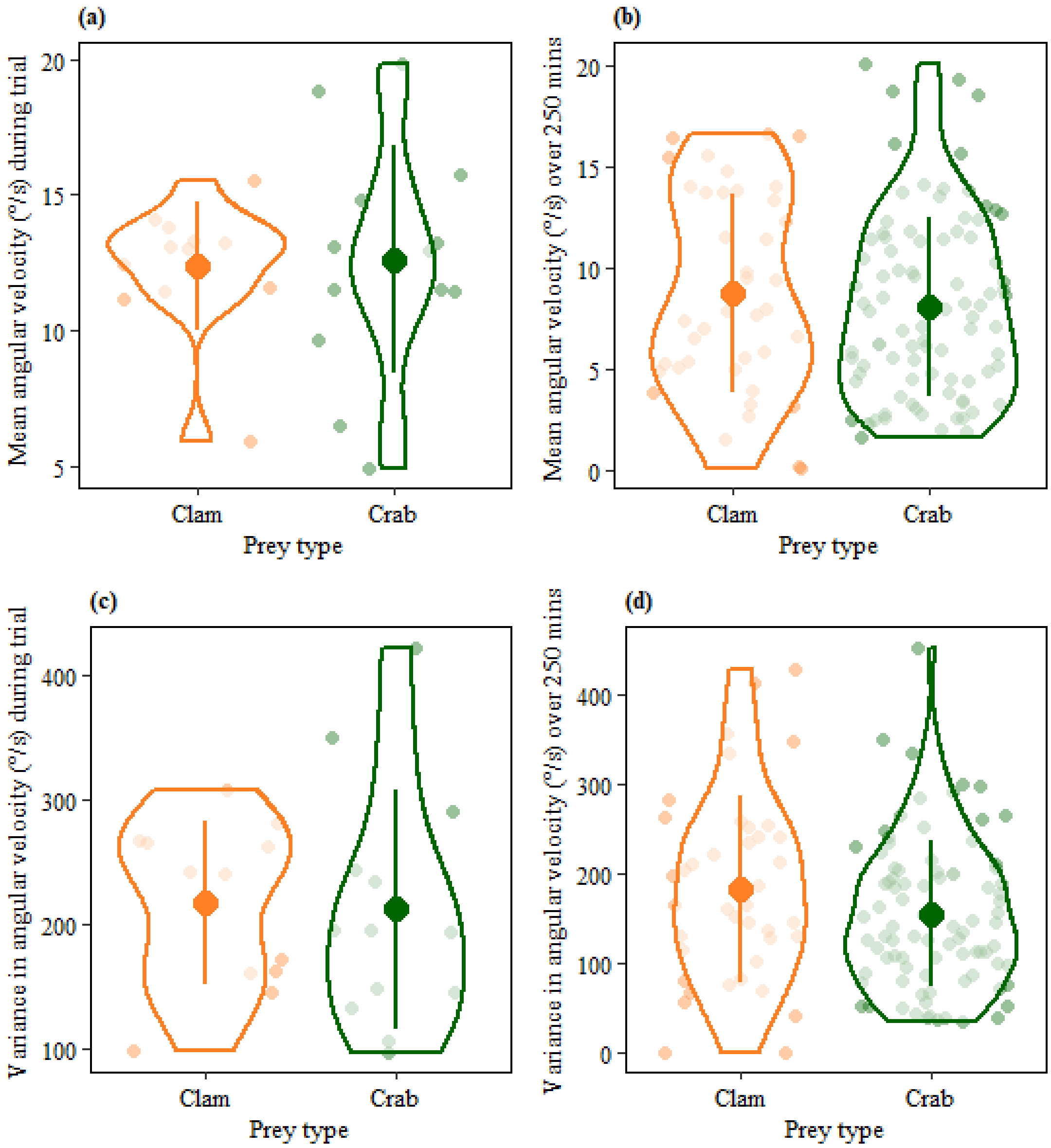

Figure 4. Rotational movement data for absolute angular velocity (AAV) for turtles in rescue centre tanks during feeding trials with clams (depicted in orange), and crabs (depicted in green). Violin plots show (a) mean angular velocity and (b) variance in angular velocity, during each 25-minute feeding trial, and (c) mean angular velocity and (d) variance in angular velocity, over a 250-minute period (starting with a 25-minute feeding trial and continuing for nearly four hours after). During trial data, plots (a, c) present data from 12 trials with clams and 13 trials with crabs; during and post-trial, plots (b, d) present data from four trials with clams and nine trials with crabs (each data point representing 25 minutes of data). The outline of the violin plot indicates point density and the central circle and line indicate the mean ± SD respectively. Plots show no obvious differences in angular velocity either during or after the experiments related to being fed clam or crab prey types; statistical analysis confirmed that there was no significant difference (Table 3, GLMMs 7 and 8).

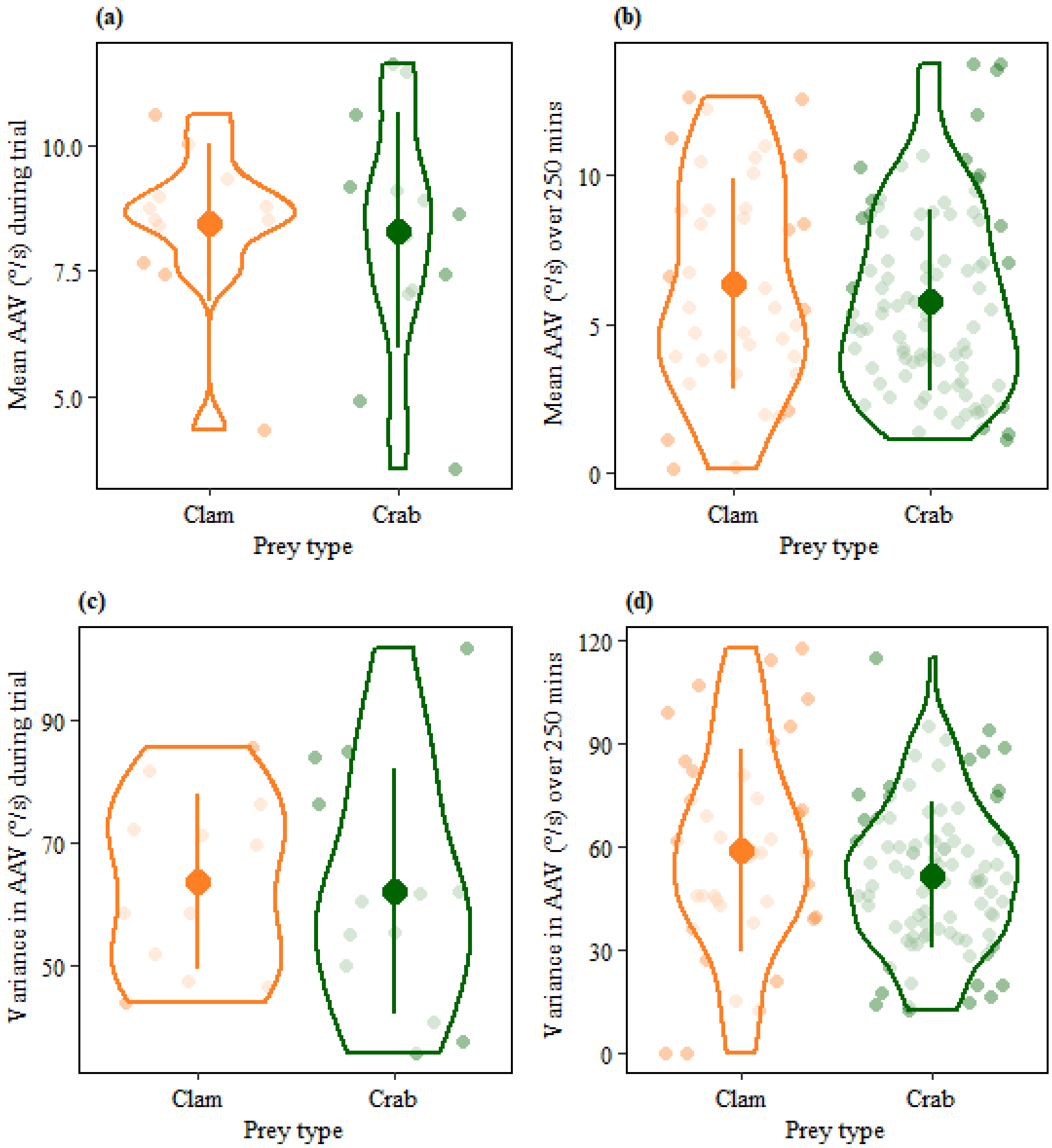

Figure 5. Rotational movement data for absolute angular velocity (AAV) for turtles in rescue centre tanks during feeding trials with clams (depicted in orange), and crabs (depicted in green). Violin plots show (a) mean AAV and (b) variance in AAV, during each 25-minute feeding trial, and (c) mean AAV and (d) variance in AAV, over a 250-minute period (starting with a 25-minute feeding trial and continuing for nearly four hours after). During trial data, plots (a, c) present data from 12 trials with clams and 13 trials with crabs; during and post-trial, plots (b, d) present data from four trials with clams and nine trials with crabs (each data point representing 25 minutes of data). The outline of the violin plot indicates point density and the central circle and line indicate the mean ± SD respectively. Although plots show no marked differences between clam and crab trials in terms of the mean and variance in AAV, the data points from crab trials are slightly wider spread during trials, however statistical analysis revealed no significant differences (Table 3, GLMMs 9 and 10).

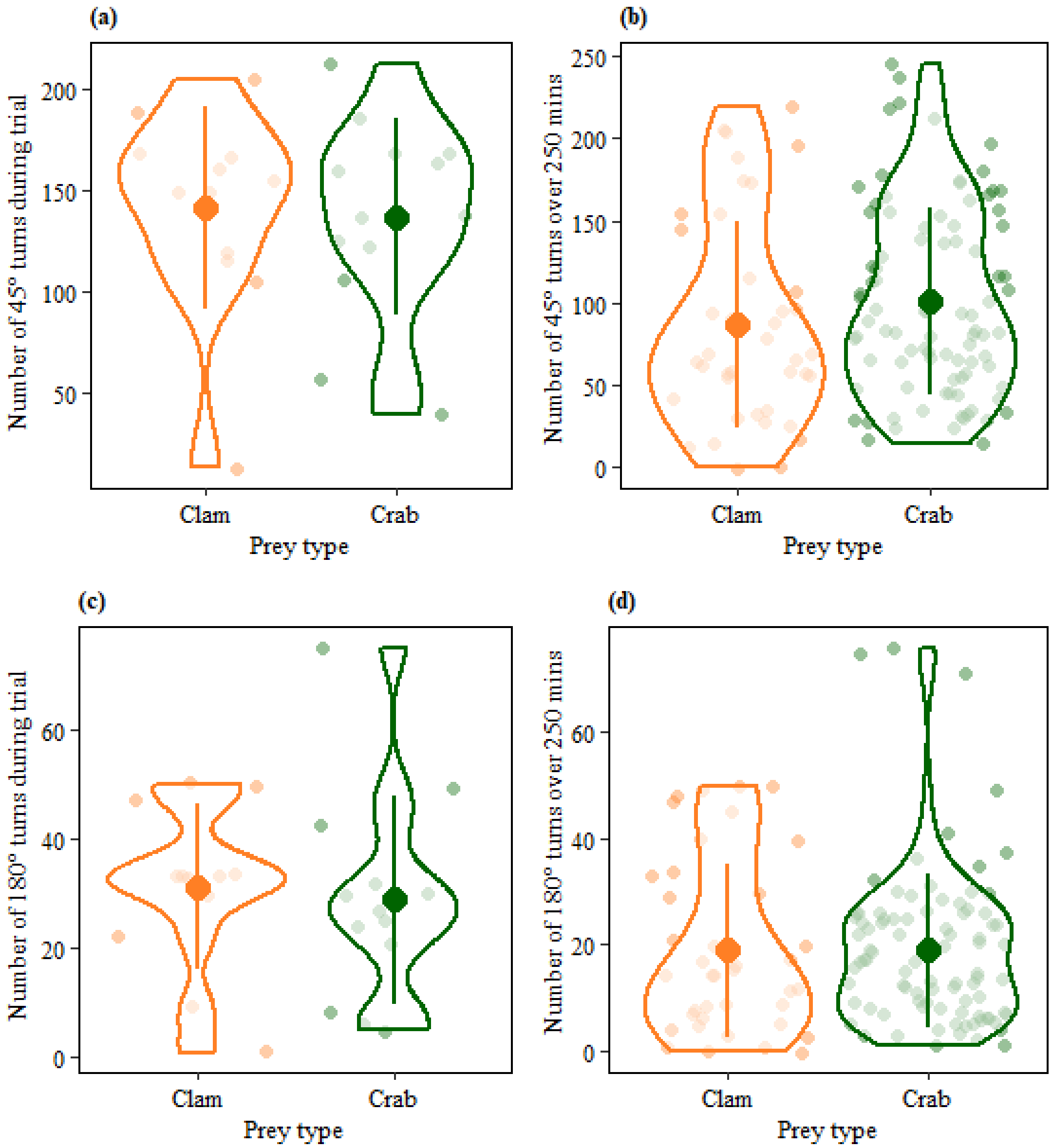

Figure 6. Turning data for turtles in rescue centre tanks during feeding trials with clams (depicted in orange), and crabs (depicted in green). Violin plots show (a, c) the number of 45° and 180° turns, respectively, during each 25-minute feeding trial, and (b, d) the 45° and 180° turns, respectively, over a 250-minute period (starting with a 25-minute feeding trial and continuing for nearly four hours after). During trial data, plots (a, c) present data from 12 trials with clams and 13 trials with crabs; during and post-trial, plots (b, d) present data from four trials with clams and nine trials with crabs (each data point representing 25 minutes of data). The outline of the violin plot indicates point density, and the central circle and line indicates the mean ± SD, respectively. Plots reveal similar turn rates per 25 minutes at both angle thresholds with obvious outliers resulting from individuals that completed very few or comparatively high

numbers of turns. Interestingly the number of 45° turns did not differ significantly depending on prey type (Table 3, GLMM 11) but the number of 180º did and was found to be significantly lower in trials with crabs (Table 3, GLMM 12).

4. Discussion

The goal of providing enrichment to animals in a controlled environment is to enhance animal welfare by the creation of added options that encourage a wider diversity of behaviour (Newberry 1995; Mellen & Sevenich MacPhee 2001; Buchanan-Smith 2010). Often, enrichment is associated with feeding, and may include the provision of live prey (Bashaw et al. 2003), as was the case in this study. Analysis *via* GLMMs revealed no significant differences in behaviour according to prey type for all of the selected metrics apart from heading variance and the rate of completion of 180º turns. This was unexpected given that crabs are more mobile than clams and it was hypothesised that turtle movement would somehow reflect this, at least during the actual feeding trials. It may be though, that the mobile neck of the turtles accounted for any movement differences between prey types with no movement being translocated to the carapace (Wilson et al. 2020b). That apart, although sample size was small, my findings strongly suggest that certain types of enrichment have little effect on activity levels or movement patterns in reptiles like turtles. These findings do not trivialise the importance of environmental enrichment (numerous enrichment studies demonstrate profound benefits for captive animals (see (Shyne 2006) and references therein), but they do highlight the importance of monitoring animal behaviour in a non-subjective, quantifiable manner as a given type of enrichment may not have the expected or desired effect.

4.1 Goals of environmental enrichment

As custodians with control over captive animal management (in terms of environmental surroundings and providing care), it is our duty to ensure the welfare of our animals (Benn et al. 2019). Appropriate nutrition, environmental stimuli and opportunities for behavioural expression are key to animal well-being and mental state (Mellor & Beausoleil 2015), especially when animals are housed individually (Burghardt et al. 1996). Species-specific behaviours must be taken into account if behavioural indicators of welfare are to be used effectively. For example, studies with box turtles (see Case et al. 2005; Alba et al. 2017) and geckos (Bashaw et al. 2016) demonstrate the need for effective enrichment strategies that meet the behavioural needs of a species (Bacon 2018). Because behaviour provides insight into an animal's well-being, or how an individual 'feels' (Bacon 2018), various types of behaviour including; exploratory, play, anticipatory, affiliative and vocalisation, may be used to assess and monitor positive emotion in reptiles to varying degrees (Boissy et al. 2007; Whitham & Wielebnowski 2013). The findings of this study demonstrate how motion- and orientation-sensitive tags can be used to quantify some of these behaviours (Shepard et al. 2013; Mosser et al. 2014; Williams et al. 2014; Wilmers et al. 2015). This approach (i.e. using multi-sensor tags and video footage to quantify behaviour (Thompson & Heithaus 2014)) could help current guidelines for the captive management of reptiles by encouraging less reliance on resource-based indicators and support a move towards incorporating animal-based indicators (which give a better indication of affective state (Benn et al. 2019)) in a reliable and standardised manner.

Exploratory behaviour is generally the easiest behaviour to observe and quantify in captive reptiles (Benn et al. 2019). Conversely, play is less often associated with ectothermic species (perhaps due to prioritizing energy for essential behaviours like hunting and basking (Paré & Lentini 2010)). Nonetheless, studies have shown that reptiles, especially larger, more long-lived species like monitor lizards and turtles, are capable of play and can even benefit from problem-solving activities (Burghardt 1990; Burghardt et al. 1996; Burghardt 2005; Manrod et al. 2008). As such, play might be a valuable welfare indicator for some reptiles (Benn et al. 2019). Although no signs of play behaviour were observed (in most of the clam and crab trials, the turtles ate the prey quickly), this may be because the experimental design was minimalistic to reduce confounding factors and did not offer an appropriate, specific stimulus for play. Although play behaviour is frequently reported in mammalian species and is often associated with food (Creel & Creel 1995; Hall & Bradshaw 1998; Baskin et al. 2015; Cecchetti et al. 2021), play behaviour is not widely reported in reptiles (Paré & Lentini 2010; Benn et al. 2019). A combination of environmental enrichment types may be more conducive to exploratory behaviour and play in turtles, with studies often using a combination of nutritional and physical enrichment such as floating structures (buoys, logs, balls and rings (Monreal-Pawlowsky et al. 2017; Kanghae et al. 2021)), submerged shelters, PVC pipes (Therrien et al. 2007), brushes fixed to pipes/tank walls and vegetation (Escobedo-Bonilla et al. 2022), to improve animal well-being and bring about behavioural responses to the additions.

Contrary to my expectations, there was no significant difference in either approach time or VeDBA between clam- and crab-feeding trials. This may have been because, although the crabs were motile (and sometimes evaded capture for a while), the clam shells were hard to eat, requiring a number of attempts to break, thus, turtles typically spent longer eating the clams. In fact, turtles typically prioritised eating the shell of the clam over the animal flesh itself, often continuing to eat shell fragments throughout the feeding trial. This affinity for the shell may be because mollusc shells are rich in calcium (so much so that they are used in the egg industry as a calcium supplement for laying hens (Finkelstein et al. 2010)). Furthermore, turtle carapaces, as well as providing protection, act as reservoirs for calcium and other essential minerals like magnesium, phosphate, and sodium, which serve to buffer the blood from acid-base disturbances when the turtles are diving (Jackson et al. 2007).

The importance of enrichment when it comes to large mammal species and reducing stereotypic behaviours is well documented (Mason & Latham 2004; Shyne 2006). In comparison, studies detailing how reptilian species benefit from increased behavioural opportunities created by enrichment are lacking (Benn et al. 2019). Nonetheless, studies have demonstrated that changes to enclosure design can reduce time spent hiding and increase activity levels in various reptilian species, illustrating the need for spatially complex enclosures for enhancing behavioural repertoires (Rose et al. 2014). Indeed, sea turtles at the ‘Arca del Mar’ rehabilitation centre were frequently observed resting by the filter pipe or hiding under basic semi-circle shelters. As such, a more complex environment may encourage more diverse behaviour. It is, however, important to recognise that treatment and easy access to animals, rather than enrichment, are the priorities at a rehabilitation centre, especially because animals are only kept for a limited period. And even though some rehabilitating animals may benefit from environmental enrichment (for example introducing stimuli to encourage swimming in order to strengthen weakened flippers), to others it may be hazardous if they got trapped or if equipment was not sanitised. It is therefore arguably more important to provide effective enrichment for animals that spend years, or their entire lives, in captivity. Investigations like this one further our understanding of how enrichment may or may not affect turtle behaviour, including activity and state, and could, with further study, help define appropriate enrichment guidelines for turtles and other animals kept in zoos and aquariums. Given that animals in the wild tend to display a wide range of behaviours not seen in captive animals (Zwart 2001; Benn et al. 2019; Chatpongcharoen et al. 2021), biologging could be used with a view to creating environments that encourage a wider range of behaviours.

The goal of environmental enrichment may not always be solely to enhance captive animal well-being. Enrichment is also regularly used to facilitate the re-introduction of animals back into the wild (Reading et al. 2013; Monreal-Pawlowsky et al. 2017). For example, an injured loggerhead that had spent 10 years in captivity was released into the wild after the implementation of an enrichment program designed to encourage natural feeding and locomotory behaviour. As testimony to the success of this approach, a transmitting device, still working 10 months post-release, showed that the turtle had travelled over 3,500 km (Monreal-Pawlowsky et al. 2017). Few studies have examined the effects of environmental enrichment in sub-adult and adult loggerhead turtles although one study found a significant increase in ‘random swimming’ and ‘focused behaviour’ and a decrease in ‘patterned swimming’ and ‘resting’ following provision of enrichment to three captive adult loggerheads, implying improved welfare for the animals (Therrien et al. 2007). Environmental enrichment may also be implemented before releasing turtles that have been reared in captivity to minimize post-hatchling vulnerabilities (Heppell et al. 1996; Bell et al. 2005) into the wild (Okuyama et al. 2014; Tetzlaff et al. 2018). Well-designed captive environments and behavioural training, such as the feeding of live prey, can be used to help individuals acquire capabilities to augment their chances of survival in the wild by stimulating wild-type behaviours (Alberts 2007; Tetzlaff et al. 2018).

4.2 Limitations and perspectives

This study illustrates how motion- and orientation-sensitive tags can be used within a human-controlled environment to quantify a variety of movement metrics. Unfortunately, the small sample size limits the reliability of these findings statistically although this is regularly the case for captivity-based studies, given that typically only small numbers of individuals are maintained in zoos and aquaria (Swaisgood & Shepherdson 2005; Kuhar 2006). Indeed, the feeding trials had to stop when all of the ‘healthy’ turtles in the rehabilitation centre were re-released into the wild (this resulted in fewer clam trials being completed). Ideally, a greater sample size, including a control group, and longer tag attachment durations or repeated measures of the same individuals, would give proper statistical credibility to the findings presented in this study. Unfortunately, limited numbers of turtles and tags made adding a control group logistically impractical. Moreover, comparisons between a control group (receiving the typical half-frozen mixture of squid, fish and vegetables), against turtles being fed crabs and clams would have been biased as all study animals still received their normal food mix after the feeding trials had ended and any effects of this would have been captured in ‘post-trial’ data. In order to have finished the feeding trials by the time that turtles were fed their normal diet, acclimatisation periods were kept short (15 minutes); ideally a delay of 1–2 hours should have been implemented (other studies include a 30-minute delay or more, often leaving several hours before recording data) as abnormal behaviours such as increasing swimming are typically observed for some time following tag attachment (Thompson & Heithaus 2014; Arkwright et al. 2020). Despite these limitations, data analysis for the majority of the investigated movement metrics indicated no significant changes in behaviour in response to prey type.

Although crabs were expected to elicit a more dynamic behavioural response, this was not the case, revealing how important it is to test pre-conceived notions regarding enrichment in the captive environment. In fact, the two significant movement metrics, variance in heading and 180º turns actually decreased with crab trials. Furthermore, if the provision of motile prey is ineffective when it comes to eliciting a desired behavioural response, the provision of live food may not be a valuable form of enrichment for sea turtles (but for certainty, this would require further study). Our study would have been improved by testing a wider variety of live and dead prey. Although hunting live prey might be enriching for carnivorous reptiles (Manrod et al. 2008; Phillips et al. 2011), it presents ethical and legal issues (Zwart 2001). A suitable replacement might be to use a floating food ball or a mechanical ball to simulate dead prey moving (Benn et al. 2019). The importance of live prey may vary greatly depending on the species in question. It is worth noting, however, that there are several examples of nutritional enrichment, even for mammalian carnivores, that do not involve live prey, for example: providing intact carcasses (Veninga & Lemon 2001 2001; McPhee 2002), artificial prey (Markowitz et al. 1995), odours/scent (Williams et al. 1999; Cohen & Moore 2001), food puzzles (Lyons et al. 1997; Jenny & Schmid 2002) and physical toys (Knowles & Plowman 2001).

It is unclear why the turtles showed no interest in jellyfish (which led to jellyfish trials being discontinued) because loggerheads are known to feed on jellyfish as well as many other types of prey including crabs, bivalves, gastropods, fishes, urchins and sponges (Tomas et al. 2001; Palmer et al. 2021). However, jellyfish do not represent an important dietary component for loggerheads (especially in the western Mediterranean), whereas crabs and clams do (Tomás et al. 2001; Palmer et al. 2021). Furthermore, loggerheads are not typically observed eating moon jellyfish, (the species used in this study), in contrast to pelagic jellyfish, *Pelagia noctiluca*, which are more commonly eaten (Plotkin et al. 1993; Bolten & Balazs 1995; Bartol & Ketten 2006). In two instances, individuals attempted to eat the shadow cast by the jellyfish on the tank floor, suggesting that the jellyfish may have been difficult for the turtles to see against the light grey-green background of the tank. This was unexpected as loggerhead turtle eyes have high spatial resolution and are well adapted to dim light in order to forage for slow-moving benthic prey (Bartol & Musick 2001; Bartol et al. 2002).

It has been proposed that creating enclosures that simulate a species' natural environment is a form of enrichment (Benn et al. 2019; Chatpongcharoen et al. 2021). A study with Eastern indigo snakes (*Drymarchon couperi*), found that they favoured river rocks (part of the species' natural environment) over PVC pipping, a sandbox, and gel stickers (the snakes showed no interest in the latter) (Mehrkam & Dorey 2015). Generally speaking, it is impossible and impractical to replicate a species natural environment properly in captivity (Zwart 2001) but bettering our understanding of reptile species habitat requirements will enable optimized enclosure design and husbandry (Benn et al. 2019). The next step for a study like this one would be to use DD tags to investigate whether various types of physical enrichment elicit different behavioural responses in sea turtles.

4.3 Future directions

As touched upon in section 4.2, it would be valuable to attach DDs to turtles under structurally enriched conditions and compare their behaviour with control turtles in barren tanks. As well as providing a more complex environment, other species could be introduced, for example adding more turtles could lead to social interactions, although this would require close monitoring of individuals as it would be unethical to keep animals together if they were showing aggression and could sustain injuries. Ideally, future studies would be carried out with sufficient study animals to reach numbers that are biologically and statistically significant to give credibility to findings. This may mean collecting data over a longer timeframe or even pooling data from different aquariums and rehabilitation centres.

Many of the issues related to animal well-being in captive care (*cf.* Rose et al. 2017a; Rose et al. 2017b; Shorter et al. 2017), including stress and stereotypic behaviours, could likely be well quantified by animal-attached devices (*cf.* Shepard et al. 2008b; Wilson et al. 2008; Whitney et al. 2010; Brown et al. 2013; Whitney et al. 2016). Reliable tools for the assessment of animal-based indicators and affective state would enable the evaluation of management procedures relating to health and the identification of well-being-related shortcomings. Reptiles are often seen as ‘behaviourally simple’ but documented environment-induced behavioural changes (Burghardt et al. 1996; Almli & Burghardt 2006; Alberts 2007; Manrod et al. 2008; Burghardt 2013; Bashaw et al. 2016) suggest that the use of tags for captive *versus* wild behavioural comparisons could be instrumental in enhancing captive environments. The application of multi-sensor tags could be made even more convenient, especially in wild environments, by using remote data collection in real time (Laske et al. 2014; Wilmers et al. 2015), both of which would reduce animal handling and speed up data analysis. Fortuitously, plenty of suitable data may already exist for wild conspecifics as logging devices have been more extensively deployed on wild animals over the last few decades (Eckert 2002; Wilson et al. 2005; Wilson et al. 2006; Quintana et al. 2007; Brown et al. 2013; Wilson et al. 2018b; Gunner et al. 2020; Williams et al. 2020; Wilson et al. 2020a; Wilson et al. 2021; Gómez-Laich et al. 2022), and could be compared with animals tagged in zoos and aquariums in order to define a set of expected behavioural states and/or activity levels.

5. Conclusion

This chapter presents data on the behavioural response of loggerhead turtles in a controlled environment during and after nutritional enrichment trials with clams and crabs. Contrary to expectations, the behaviour of turtles did not change significantly with prey type for the majority of the movement metrics tested (there was only a significant difference for heading variance and the number of 180º turns). Investigations like this one help further our understanding of how enrichment may, or may not, affect turtle behaviour and challenge ingrained perceptions of what is important in a captive environment. Collecting behavioural information, (as done in this study), for various species housed in zoos and aquariums could help staff create environments that elicit desired behaviours or activity levels, whether they are of a wild-type nature or not. Considering that the maintenance of animals in captivity (particularly large mammals and other vertebrates) is frequently under scrutiny (Keulartz 2015), objective measures of well-being would prove valuable husbandry tools.

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Chapter 5

Comparing movement behaviour in captive and free-living loggerhead turtles *via* animal attached devices

Abstract

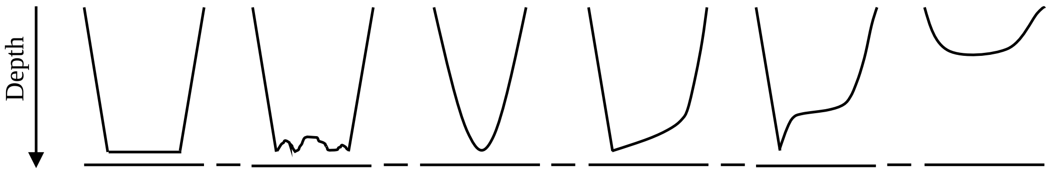
A huge amount of literature exists based on devices attached to wild animals and these have transformed our understanding of animal behaviour, physiology, and movement ecology. Animal-attached devices are currently less commonly used within a captive setting even though many issues related to animal well-being in captive care, including, stress, stereotypic behaviours, and assessing the extent to which captive and wild-type behaviours overlap, could potentially be well quantified by this approach. In this study Daily Diaries (DDs, motion-sensitive tags), were used to compare the behaviour of 'healthy' loggerhead turtles, *Caretta caretta*, in managed care with free-living loggerhead turtles. Specifically, turtle behaviour during the 'bottom phase' of dives was compared between two managed care scenarios (rescue centre tanks and structurally diverse aquarium exhibits) and the wild. The aim being to find out if and how movement behaviour between the three scenarios differed and whether it was pertinent to make inferences about 'wild-type' behaviours based on the assessment of turtle behaviour in managed care. Interestingly, there were no significant difference in activity (assessed *via* the vector of the dynamic body acceleration, VeDBA) between the environments. There were, however, significant differences between managed care and free-living turtles for several of the movement metrics studied, including pitch variance, heading variance and absolute angular velocity (AAV) as well as the number of turns per hour reaching extents of 45º, 90º, 180º and 360º. Explanations for this are discussed, as well as consideration of the potential of motion-sensitive tags to assess movement behaviours for captive species with a view to creating environments that elicit more normal behaviours and levels of activity.

1. Introduction

An understanding of animal movement gives researchers powerful insights into a suite of issues including; effective conservation (Wilson et al. 2008; Bograd et al. 2010; Wilson et al. 2015), impacts of land-use change (Patz et al. 2004; Dale et al. 2014; Allen et al. 2017), the spread of invasive species (Crowl et al. 2008; Vander Zanden & Olden 2008), and zoonotic diseases (Patz et al. 2004; Marano et al. 2007; Han et al. 2015), as well as species-specific behaviours and requirements (Ropert-Coudert & Wilson 2005; Shepard et al. 2008b; Wilson et al. 2008; Fossette et al. 2010; Brown et al. 2013; Wilson et al. 2017). Unfortunately, quantification of animal movements can be challenging, particularly for cryptic species and those that inhabit environments where direct observation is difficult or even impossible, i.e., in aquatic, arboreal and aerial systems (Shepard et al. 2008b; Wilson et al. 2008; Whitney et al. 2010; Brown et al. 2013).

In such circumstances, animal-attached devices such as time depth recorders (TDRs), satellite tags and movement-sensitive loggers have provided researchers with valuable information, especially when it comes to diving vertebrate behaviour (Hays et al. 2000; Shepard et al. 2006; Hays et al. 2007; Tyson et al. 2012; Goldbogen et al. 2013; Irvine et al. 2017; Shearer et al. 2019). For example, animal-attached devices have played a central role in our understanding of sea turtle behaviour, revealing how individuals spend the majority of their time at depth (Hochscheid et al. 1999; Hart et al. 2010; Okuyama et al. 2014; Wilson et al. 2017). Information on depth use over time obtained *via* TDRs has been frequently used to create dive profiles elucidating activity and depth-related movement behaviour (Eckert et al. 1986; Hays et al. 2000; Houghton et al. 2002; Rice & Balazs 2008). Dive profiles have been classified into five types based on their shape in plots of depth against time (Figure 1) (Minamikawa et al. 1997; Hochscheid et al. 1999; Hays et al. 2000; Houghton et al. 2002; Wilson et al. 2017).

Dive type is considered indicative of behaviour. For example, U-shaped dives with a flat bottom (Figure 1; dive type 1a) are associated with resting behaviour on the seafloor and energy conservation (Minamikawa et al. 1997; Hochscheid et al. 1999; Hays et al. 2000; Houghton et al. 2002). Undulating U-shaped dives (Figure 1; dive type 1b), however, are associated with travel along an uneven seafloor and foraging (Hays et al. 2001; Houghton et al. 2002). The remaining dive types, V- and S-shaped dives (Figure 1; dive types 2, 3 and 4), are thought to be indicative of bouts of higher speed travel and periods of foraging and mid-water resting, respectively (Minamikawa et al. 1997; Hochscheid et al. 1999; Minamikawa et al. 2000). Whilst the specific amount of movement (activity) for a given dive type is likely to vary (Houghton et al. 2002; Gunner et al. 2020), the extent to which behaviours may vary for a given dive type, especially when depth is constant, has been subject to conjecture (Seminoff et al. 2006; Blumenthal et al. 2010). This is because, although TDRs indicate that several behaviours may occur within a single dive (Houghton et al. 2002), they only provide movement data in the vertical axis and so are inadequate to quantify turning behaviour, for instance (Gunner et al. 2020).



Type 1a: U-shaped dive with a steep descent, a flat bottom phase and a steep ascent.

Type 1b: U-shaped dive with a steep descent, an undulating bottom phase and a steep ascent.

Type 2: V-shaped dive with a steep descent, little or no bottom phase and a steep ascent.

Type 3: Dive with a steep descent phase, followed by a gradual ascent and a steep final ascent.

Type 4: S-shaped dive with a period of fast descent followed by a more gradual ascent. Similar to type 3.

Type 5: Shallow, sub-surface dive with a gradual descent and ascent.

Figure 1. Five dive types, classified according to typical dive profiles (adapted from Houghton et al. (2002)). For further detail regarding classification criteria see Houghton et al. (2002).

The tagging community is now addressing this weakness by including more sensors in animal-attached devices. For example, TDRs and carapace-mounted video recorders have demonstrated that a range of behaviours may be exhibited over the course of a dive (Seminoff et al. 2006) and high-frequency tri-axial accelerometers (Hussey et al. 2015; Wilmers et al. 2015) have revealed how different portions of turtle dive profiles are associated with underwater buoyancy control, depth use and movement dynamics (Hays et al. 2007; Fossette et al. 2010). Over the course of a dive, however, a turtle may allocate a large proportion of its time-budget to gliding at a more or less constant speed (Wyneken 1997; Walker & Westneat 2000; Martin 2003) or moving slowly during the ‘flat bottom’ phase of U-shaped dives (Figure 1; dive type 1a) (Gunner et al. 2020). This results in minimal changes in acceleration, making the identification of behavioural changes *via* accelerometry alone, challenging (Eckert 2002; Wilson et al. 2019). Magnetometers (Williams et al. 2017) however, can resolve rotational body movement (heading and yaw), providing data on an otherwise missing movement dimension (Noda et al. 2012; Gunner et al. 2020). Indeed, Gunner et al. (2020) demonstrated the value of compass heading for interpreting the behaviour of free-ranging sea turtles, concluding that oscillating yaw movements indicated foraging, whilst complete revolutions about the longitudinal axis, i.e. circling behaviour, indicated conspecific interactions.

Although animal-attached tags on taxa such as turtles have been pivotal for elucidating the behavioural ecology of wild animals, tag-based studies are uncommon in captive settings (Mazzaro & Dunn 2009; Ismail et al. 2012; Wilson et al. 2013b; Williams et al. 2014; Bouyoucos et al. 2017), despite their potential. This is curious because devices are relatively easy to deploy and retrieve (Bidder et al. 2014) and animals can be trained to participate by performing a desired behaviour (Ward & Melfi 2015; Shorter et al. 2017). In addition, many of the issues related to animal welfare and well-being in captive care (Hill & Broom 2009), including, stress (Wiepkema & Koolhaas 1993), the occurrence of stereotypic behaviours (Mason & Latham 2004; Mason & Rushen 2008), and assessing the extent to which captive and wild-type behaviours overlap (Veasey et al. 1996a,b), could be well quantified by animal-attached devices (Wilson et al. 2014; Pagano et al. 2017).

This study used Daily Diaries (DDs), motion- and orientation-sensitive tags to compare the behaviour of ‘healthy’ loggerhead turtles, *Caretta caretta* under three different scenarios; (i) housed in rescue centre tanks of a limited size (2–6 m diameter and 0.95 m deep), (ii) held in larger and more structurally diverse aquarium exhibits and (iii) free-living. Although wild turtles have an almost unlimited 2-dimensional space and an extended 3-dimensional space in which to roam, both wild and captive animals are able to perform U-shaped dive ‘bottom phase’ behaviours during which they may change heading (yaw) unhindered. As such, comparisons between scenarios were based on this, particularly capitalising on the angular velocity across all three axes of rotation (pitch, roll and yaw) to calculate the ‘absolute angular velocity’, (AAV), a proxy proposed as sensitive to activity in turtles to great effect (Gunner et al. 2020). Given the marked differences between the managed care and wild environments, I was interested to see if 'bottom phase' movement differed significantly between scenarios and whether it was pertinent to make inferences about energy expenditure and 'wild-type' behaviours based on the assessment of animals in captivity as has been done previously in a variety of species, both terrestrial, like giraffes, horses, big cats and deer (Veasey et al. 1996a,b; Butler & Jones 1997; Mosser et al. 2014; Williams et al. 2014) and aquatic, including seals, whales, sea turtles and penguins (Fedak et al. 1988; Butler & Jones 1997; Williams et al. 2000; Sparling & Fedak 2004; Williams et al. 2019).

The aims of this study were to compare the following movement metrics in captive and free-living turtles over a 24-hour period to account for diurnal changes in behaviour:

i. *Activity or proxies for energy expenditure* measured using the vector of the dynamic body acceleration, VeDBA (Qasem et al. 2012). Individuals in managed care were expected to have much lower VeDBAs than their wild counterparts, given the limited area in which they could move and the lack of stimuli, especially inside barren rescue centre tanks.

ii. *Variation in pitch, heading and roll*. Individuals held in rescue centre tanks were expected to exhibit fewer directional changes across pitch, heading and roll than individuals in more complex environments.

iii. *Angular movement* assessed *via* AAV and the total number of turns per hour. Turtles in barren rescue centre tanks were expected to have a lower AAV and to turn less than animals in environments with greater complexity (i.e., aquarium exhibits or the wild).

2. Methods

2.1 Study locations and animals

All the loggerhead turtles studied within a controlled environment (n = 11) were maintained at the Oceanogràfic Aquarium in Valencia, Spain, and the 'Arca del Mar' rehabilitation centre that forms part of the complex. All but one of the 'controlled environment' study animals were bycaught in gillnet and trawling fisheries off the Valencian coast and were housed at the rehabilitation centre;

Rosita, one of three turtles tagged in exhibits, is a permanent feature at the aquarium (see Table 1 for details). Turtles were brought to the centre by veterinary staff who would collect the animals from fishermen who encountered them in their nets. Upon admission, animals underwent a comprehensive health assessment including a physical examination, blood sample analysis and imaging studies when required. All turtles were examined regardless of if they had visible signs of disease or trauma; animals were considered 'healthy' if they were free of afflictions upon entry. Animals that entered with bycatch-related injuries such as gas emboli (GE; see Table 1) received the appropriate treatment following diagnosis and GE severity, a common issue in bycaught turtles (Fahlman et al. 2017), was scored following methods detailed in García-Párraga et al. (2014). Gas emboli may form in response to a rapid decrease in pressure during ascent which causes nitrogen within the tissues to bubble out, resulting in GE within the body's blood vessels, tissues and organs (Doolette & Mitchell 2001; Francis & Mitchell 2002; Vann et al. 2011). All animals were maintained at the rehabilitation centre until their blood samples and behaviour indicated that they had recovered and were fit for release.

For the purposes of this study, only animals that were admitted with minor or no signs of disease/injury were included. Furthermore, turtles were only tagged once they were 'healthy' according to veterinary assessment. The use of managed care animals was approved by the Oceanogràfic Animal Care & Welfare Committee (OCE-16-18) and the Swansea University, Animal Welfare Ethical Review Body (STU_BIOL_82015_011117151527_1).

The turtle identification numbers used throughout this manuscript are a running count of the number of turtles which were admitted to the facility across time, preceded with a 'T'. The turtles tagged at the centre were held in cylindrical rescue centre tanks, 2–6 m in diameter and with a water depth of 0.95 m. When there were too many admissions to house turtles individually, tanks were divided into two by a central barrier. As such, the movement behaviour of study animals was investigated in tanks with varying available water masses: 1,500 L, 3,000–3,500 L, 6,000 L and 19,000 L.

Table 1. Summary information of all turtles tagged within a controlled environment; column headings from left to right detail the turtle identification number, origin (i.e., bycatch location), turtle weight (kg), curved carapace length (CCL), curved carapace width (CCW), bycatch gear, state of health upon entry, date of tagging, tank size given as the available water volume (L) and the state of health when tagged. Upon arrival, a veterinary health assessment categorised animals as, 'healthy' (i.e. free of injury and disease) or with very mild to moderate gas emboli (GE) which was scored following methods detailed in García-Párraga et al. (2014) and Fahlman et al. (2017). All animals were healthy when tagged. If a turtle was tagged in an exhibit this is indicated after the tank size; turtles tagged in an outdoor exhibit with seals are indicated with an '' and turtles tagged in an indoor tank with deep sea shark species and other fish and 3D structures are indicated with an '**'. Rows with ' " ' indicate that a turtle was tagged twice, and the information is replicated in the row above. Turtle identification numbers are a running count of the number of turtles across time; T234 was admitted once and was then recaptured in 2019. The table is ordered according to turtle entry date; entry to and release dates from the rehabilitation centre, as well as the date of tagging, are provided in Appendix H.*

Turtle ID	Origin	Weight (kg)	CCL (cm)	CCW (cm)	Bycatch gear	State of health upon entry	Tagging date	Tank size (L)	State of health when tagged
Rosita	NA	78	73	73	NA	Healthy	30/01/18	991900*	Healthy
T359	Benicarlo	20.8	52	50	Trawl/bottom fishing	Moderate GE	09/02/18	6000	Healthy
"	"	"	"	"	"	"	12/02/18	7210000**	Healthy
T362	Cullera	13	42	36	Trawl/ bottom fishing	Moderate GE	09/02/18	3500	Healthy
"	"	"	"	"	"	"	12/02/18	7210000**	Healthy
T396	Vinaroz	22	59	49	Trawl/ bottom fishing	Healthy	08/05/18	6000	Healthy
T405	Peniscola	34.24	64	59	Trawl/ bottom fishing	Very mild GE	29/06/18	19000	Healthy
T234	Burriana	86	83	77	Trawl/ bottom fishing	Mild GE and fishing hook ingestion	10/10/19	12300	Healthy
T459	Burriana	12.15	45	40	Trawl/ bottom fishing	Healthy	05/03/19	3500	Healthy
T476	Vinaroz	15	49	47	Trawl/ bottom fishing	Healthy	04/06/19	3500	Healthy
T481	Cullera	25.18	64	50	Trawl/ bottom fishing	Healthy	04/06/19	3500	Healthy
T482	Peniscola	30	56	56	Trawl/ bottom fishing	Moderate GE	11/06/19	3500	Healthy
T484	Peniscola	13.53	48	43	Trawl/ bottom fishing	Mild GE	11/06/19	3500	Healthy

Free-living loggerhead turtles (n = 5) were tagged on Boa Vista Beach, Cape Verde Islands (15°58'22" N, 22°47'56" W). These animals were all adult females, tagged during inter-nesting intervals.

2.2 Data collection

All managed care turtles were fitted with Daily Diary loggers (DDs), motion- and orientation-sensitive tags between January 2018 and June 2019. The DDs logged: tri-axial accelerometery, tri-axial magnetic field strength, ambient temperature and pressure at 20 Hz per channel (Wilson et al. 2008). Acceleration was logged with respect to gravity (approx. 1 *g*), range; ± 16 *g* and magnetometry was recorded in Gauss (G) at 0.73 mG/LSb resolution, range (± 0.88 G). Both acceleration and magnetic field strength were recorded along three orthogonal axes which correspond to the dorso-ventral, lateral, and anterior-posterior axes of the animal (Williams et al. 2017). For accelerometry data, i.e. translational/linear movement, x, y and z axes give the heave, surge and sway respectively; for magnetometry data which shows postural angular rotation, the x, y and z give pitch, roll and yaw respectively (Williams et al. 2017). The devices weighed between 25–40 g and were approximately 60 x 40 x 19 mm, (size varied by ± 10 x 10 x 6 mm). Tags were glued to the second central scute of turtles' carapaces using a two-part epoxy (Veneziani Subcoat S), pre-mixed in water. When possible, healthy animals were tagged soon after arrival and just before being released into a rescue centre tank.

Free-living turtles, tagged between July and August 2014, were also fitted with DDs, recording the same set of channels but at 40 Hz. The tags were fitted just after each female turtle had finished laying eggs. As with managed care animals, the devices were attached to the second dorsal scute using a water-resistant epoxy resin glue. These devices were retrieved after a single inter-nesting interval, approximately a couple of weeks after being deployed. No biometric data exist for free-living turtles.

2.3 Data analysis

Initially tag data were visualized using custom-made software, ‘Daily Diary Multi Trace’ (DDMT) (open source, http://www.wildbyte-technologies.com). DDMT displays accelerometry, magnetometry, pressure and temperature channels on the y-axis and time on the x-axis. The software can also display useful derivatives from the primary data, including the vector of the dynamic body acceleration, VeDBA (Qasem et al. 2012), a powerful proxy for energy expenditure (*cf*. Halsey et al. 2011a; Halsey et al. 2011b; Wilson et al. 2020), and differentials (i.e., rate changes) and run smoothing windows through any desired channel. Furthermore, the occurrence of specific behaviours can be searched for *via* Boolean-type, time-based behavioural expressions (Wilson et al. 2018).

2.4 Computation of metrics

Following aims i., ii. and iii. (see above), the computation of VeDBA, pitch, roll, animal heading, absolute angular velocity and turn extent is detailed below. Using DDMT software, selected metrics for the comparison of captive and free-living turtle behaviour were smoothed over two seconds to reduce noise and then undersampled to 1 Hz in RStudio (version 3.6.0, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/) for further analysis. This was done because turtles are typically slow moving with VeDBAs usually below 0.08 g (Gunner et al. 2020) and to facilitate analysis.

2.4.1 Computing acceleration components

The ‘static’ component of acceleration due to gravity, (which amounts to 1 g or 9.81 ms^{-2}) was calculated by sending a moving average of a given window size (w) through a given sample (S_i) of each orthogonal channel's acceleration (Fang et al. 2005). A two second window was used in this study (the same was implemented by Shepard et al. (2008a)).

$$S_i = \frac{1}{w}\sum_{j=i-\frac{w}{2}}^{i+\frac{w}{2}} S_j$$

The ‘dynamic’ component of acceleration was derived by subtracting the static acceleration of each axis from the raw acceleration for that axis (Bidder et al. 2015; Gunner et al. 2020). VeDBA (*g*), used as a measure of energy expenditure, was then calculated by taking the vectorial sum of the dynamic acceleration (*DA*) values from the three orthogonal axes *x, y* and *z* (Qasem et al. 2012).

$$VeDBA = \sqrt{DA_x^2 + DA_y^2 + DA_z^2}$$

2.4.2 Computing pitch and roll

Pitch and roll (°/s) were calculated according to the static acceleration of the *x, y,* and *z* channels, which correspond to the heave, surge and sway axes and were denoted S_x, S_y and S_z respectively (Bidder et al. 2015). Note: the *‘atan2’* function computes the angle between two coordinates given as arguments that are separated by a comma and is accessible in both Microsoft Excel and Matlab (Bidder et al. 2015).

$$Pitch = \left(atan2\left(S_x, \sqrt{S_y \bullet S_y + S_z \bullet S_z}\right)\right) \bullet \frac{180}{\pi}$$

$$Roll = \left(atan2\left(S_y, \sqrt{S_x \bullet S_x + S_z \bullet S_z}\right)\right) \bullet \frac{180}{\pi}$$

$$atan2(y, x) = 2\ arctan \frac{y}{\sqrt{x^2 + y^2}\ +\ x}$$

2.4.3 Computing animal compass heading

Animal compass heading (also referred to as ‘heading’) was computed within a 0–360° range; a heading of either 0° or 360° equated to Magnetic North (Gunner et al. 2020). Prior to the computation of heading, distortions to the local magnetic field were compensated for in DDMT. Using calibration data, which is generated by rotating the DD about all orientations of roll, pitch, and yaw and forms a sphere on a tri-axial magnetic field intensity scatterplot, DDMT has a reference frame for the vectorial sum of magnetometry data across the ‘x’, ‘y’ and ‘z’ axes (Williams et al. 2017). The reference frame is then used to correct for ‘hard-iron’ distortions, which cause the sphere to migrate from its origin and ‘soft-iron’ distortions which cause the sphere to become ellipsoid in shape (Gebre-Egziabher et al. 2006; Ozyagcilar 2012; Gunner et al. 2020). *Via* an ellipsoid-fitting algorithm and a correction factor, spherical fields were returned to their true origins and deformations in shape were corrected (Bidder et al. 2015; Walker et al. 2015).

Angular rotation across pitch and roll axes was used in the tilt correction procedure on each orthogonal magnetometer channel (Bidder et al. 2015). Compass data were normalised before each orthogonal channel was rotated according to pitch and roll; thus ensuring that the magnetometry channels were compensated, accounting for changes in angle resulting from postural offsets, with values corrected to give a horizontal co-ordinate frame (Bidder et al. 2015). Compass heading (*H*) with respect to Magnetic North could then be computed:

$$H = mod\left(360 + \left(atan2(-m_y, m_x) \bullet \frac{180}{\pi}\right), 360\right)$$

where *mod* is the modulo operator and m_y,m_x are the normalized, ellipse fitted and co-ordinate frame-adjusted *x* and *y* channels of the magnetometer respectively (Bidder et al. 2015; Gunner et al. 2020).

Heading was then converted from degrees to Cartesian coordinates to overcome issues when calculating the arithmetic mean arising from the circular nature of yaw data, i.e., both 0° and 360° define the same point (Magnetic North) on a circle (Pewsey et al. 2013). The arithmetic mean of individual angles ($\hat{\theta}$) was then calculated from sample trigonometric moments and the resultant units restored back to degrees ($\widehat{H}$). For more information concerning the calculation of pitch, roll and compass heading see Walker et al. (2015), Bidder et al. (2015) and Gunner et al. (2020).

$$\hat{\theta} = atan2\left(\frac{1}{n}\sum_{j=i}^{n} sin\left(H_j \bullet \frac{\pi}{180}\right), \frac{1}{n}\sum_{j=i}^{n} cos\left(H_j \bullet \frac{\pi}{180}\right)\right)$$

$$\widehat{H} = mod\left(360 + \left(\hat{\theta} \bullet \frac{180}{\pi}\right), 360\right)$$

2.4.4 Computing absolute angular velocity

The absolute angular velocity, AAV (°/s), movement metric integrates pitch, roll and yaw axes to give the absolute instantaneous angular velocity (Gunner et al. 2020). A two second smoothing window was passed through the values of the three axes using a stepping range of one second before the differential angular velocities about the yaw, pitch and roll axes were created; these were denoted: '*DAVY'*, '*DAVP'* and '*DAVR'*, respectively.

$DAVP = x_{j+1} - x_j$

$DAVR = x_{j+1} - x_j$

$DAVY = x_{j+1} - x_j$

where *x* is the *ith* value of pitch/roll/yaw (Gunner et al. 2020).

$$AAV = \sqrt{(DAVP^2 + DAVR^2 + DAVY^2)}$$

Given that heading is cyclical without a true zero, high and low values were arbitrary. A logical expression for the *DAVY* prevented the rate of change surpassing 180°/s, in order to be able to tell whether an animal had turned in a clockwise or anti-clockwise direction (Gunner et al. 2020). The velocity and turn speed of the study animal need to be considered when setting the sampling interval of *DAVY*; theoretically sampling intervals should be under the time the animal in question would take to complete a 180° turn in order to avoid errors when computing the rate change (Gunner et al. 2020). Thus, turning 180° was the greatest achievable angle for any given axis per second.

The *DAVY* was also used to determine every time a turtle reached an angle threshold of 45°, 90°, 180° and 360°. Turn extent was measured using conditional running cumulative sum functions in RStudio; these reset each time the condition, i.e., the angle threshold, was reached.

2.5 Defining U-shaped dives for data selection

Behavioural comparisons between free-living and managed care turtles were based on U-shaped dive 'bottom phase' behaviour because, unlike the other dive types and stages (*cf*. Figure 1), this can be performed by animals in both groups. Individuals maintained within rescue centre tanks had a limited space in which to move (2–6 m diameter and 0.95 m deep) and were frequently observed resting on the bottom of the tank. Nonetheless, in order to eliminate surfacing events and behaviour, only data from the deeper half of the pressure range (recorded for each turtle) was used in 'bottom phase' analysis. The same protocol was adopted for the managed care turtles tagged in exhibits because internal structures resulted in a highly variable exhibit depth, making it difficult to separate sub-surface swimming and 'bottom phase' data (maximum exhibit depth was approximately 6.5 m deep).

Free-living turtles, which had an almost unlimited 2-dimensional space and an extended 3-dimensional space in which to roam, performed a variety of dive types. For these, the bottom phase of flat U-shaped dives, (also known as resting dives (Houghton et al. 2002)), was extracted from wild turtle datasets for behavioural comparisons. Dives from which 'bottom phase' data was obtained were all deeper than three metres to filter out subsurface swimming (Gunner et al. 2021). The U-shaped dive criteria was set out and data extraction was performed by Gunner et al. (2021), who found that rest constituted a significant proportion of each turtle's time budget but that dives were often episodic, with bouts of activity amounting to 16–38 % of the elapsed time (Gunner et al. 2021).

Data for this study were analysed from 11 turtles in managed care (see Table 1) and five free-living, inter-nesting females. For each individual included in this study, 24 hours of bottom time data were selected, this was done by adding data from the bottom phase of sequential U-shaped dives to total 24 hours of data. For animals in captive environments, the 24 hours commenced after a 1-hour acclimatisation period. The bottom phase data were sequentially added together because the proportion of 'bottom time' during the first day of tagging was very low for the free-living turtles, leaving scarce data for the comparison of movement behaviours.

2.6 Statistical analysis

Multiple generalized linear mixed-effects models (GLMMs) were conducted to examine whether the behaviour of turtles differed significantly depending on whether they were free-living (the baseline point of reference; n = 5), in rescue centre tanks (n = 10) or in aquarium exhibits (n = 3). The three scenarios were modelled as the explanatory variable and the behavioural response, assessed *via* several movement metrics, were incorporated as fixed effect continuous covariates. Turtle ID was incorporated into every GLMM as a random effect to account for inter-individual differences such as turtle weight and sex. The selected movement metrics included: mean VeDBA, variance in VeDBA, variance in pitch and roll (plus their respective differentials), variance in heading, cumulative AAV, variance in AAV and the total number of turns reaching angle extents of 45º, 90º, 180º and 360º. These metrics were sampled at hourly intervals and were calculated for each turtle over a 24-hour period (starting one-hour post tagging for managed care turtles), yielding 24 data points per individual. A GLMM was run for each of the movement metrics in order to negate multicollinearity, which may occur if similar metrics are built into the same model (Pitt & Myung 2002). The means of pitch and roll variables were not assessed because small offsets in baseline values caused by inter-individual differences in turtle size, carapace slope and sensor inclination (Gunner et al. 2020) could not be corrected as turtles did not remain still after tagging.

The GLMMs were performed using the ‘glmer’ function from the ‘lme4’ package in R (Bates et al. 2014) and were fit using either a Gaussian, gamma or Poisson family (the variance function) and a log link (a transformation of the mean of the response variable), depending on what best suited a variables’ distribution. Given that all models were run with a log link, statistically significant coefficient estimates were exponentiated for interpretation within the text.

Diagnostic plots and Akaike Information Criterion (AIC) were used to determine the best fitting model (both ‘null’ and ‘full’ models are presented in results). The ‘summary’ function was used to obtain *p*-values, which were used as a measure of significance for the coefficient estimates. Because the explanatory variable had three levels (free-living, tanks and exhibits), Tukey post-hoc tests were carried out using the ‘glht’ and ‘summary’ functions from the ‘multcomp’ package (Hothorn et al. 2008) in order to obtain a pairwise comparison for tank and exhibit turtles as well as free-living and tank *and* free-living and exhibit (the latter two could be analysed as part of GLMM outputs). All graphical representation was carried out using the ‘ggplot2’ package (Wickham 2016).

3. Results

Data from 16 turtles were included in this study; 11 animals were tagged in a managed care environment (two of these individuals were tagged twice resulting in 13 tagging sessions– ten in rescue centre tanks and three in aquarium exhibits) and a further five animals were tagged in the wild. The turtles tagged in managed care were all large juveniles (45–64 cm curved carapace length, CCL) apart from two adult females, Rosita and T234, (73 cm and 83 cm CCL respectively; *cf*. Table 1), whereas the turtles tagged in the wild were all adult females in the inter-nesting phase (for which no biometric data were collected). Bottom phase data from turtle dives were sequentially added together until there were 24 hours of data for each study animal. This was done because the proportion of ‘bottom time’ for the free-living turtles on the first day of tagging was very low, leaving insufficient data for behavioural comparisons between environments (Table 2). Bottom phase data were then graphed in order to compare specific movement behaviours across the three environments.

Table 2. Summary information for all captive and wild turtles that were tagged as part of this study, showing the turtle ID, turtle weight (kg), tank size as the available water volume (L) and the total hours and percentage bottom time of turtles during the first day of tagging. Note how wild turtles had a much lower percentage bottom time than managed care turtles, irrespective of turtle weight or whether animals were in rescue centre tanks or exhibits.

Turtle ID	**Turtle weight (kg)**	**Tank size (L)**	**Bottom time (total hours)**	**Bottom time %**
Rosita	78	991900*	20.27	84.47
T359	20.8	6000	22.49	93.71
"	"	7210000**	20.94	87.23
T362	13	3500	22.21	92.52
"	"	7210000**	17.78	74.08
T396	22	6000	22.06	91.93
T405	34.24	19000	19.06	79.42
T234	85.5	12300	19.38	80.75
T459	12.15	3500	21.55	89.78
T476	15	3500	20.36	84.83
T481	25.18	3500	17.09	71.20
T482	30	3500	18.97	79.03
T484	13.53	3500	20.64	85.98
Wild 1	NA	NA	0.56	2.33
Wild 2	NA	NA	2.44	10.17
Wild 3	NA	NA	0.92	3.84
Wild 4	NA	NA	4.28	17.85
Wild 5	NA	NA	14.53	60.53

3.1 Activity

Turtles tagged in rescue centre tanks generally had slightly lower VeDBAs than turtles tagged in exhibits or the wild (Figure 2). However, animals in both of the managed care environments (i.e., tanks and exhibits) had a wider range in VeDBA values, with some individuals exhibiting particularly high mean VeDBA and variance in VeDBA per hour in comparison with the free-living individuals. Despite this, GLMMs revealed no significant difference in either mean VeDBA or VeDBA variance (Table 3, GLMMs 1 and 2 respectively). Post-hoc analysis comparing both the mean VeDBA and the VeDBA variance of turtles in the wild *vs* tanks, wild *vs* exhibits and tanks *vs* exhibits also found no significant differences between the three environments (Table 4, GLMMs 1 and 2 respectively).

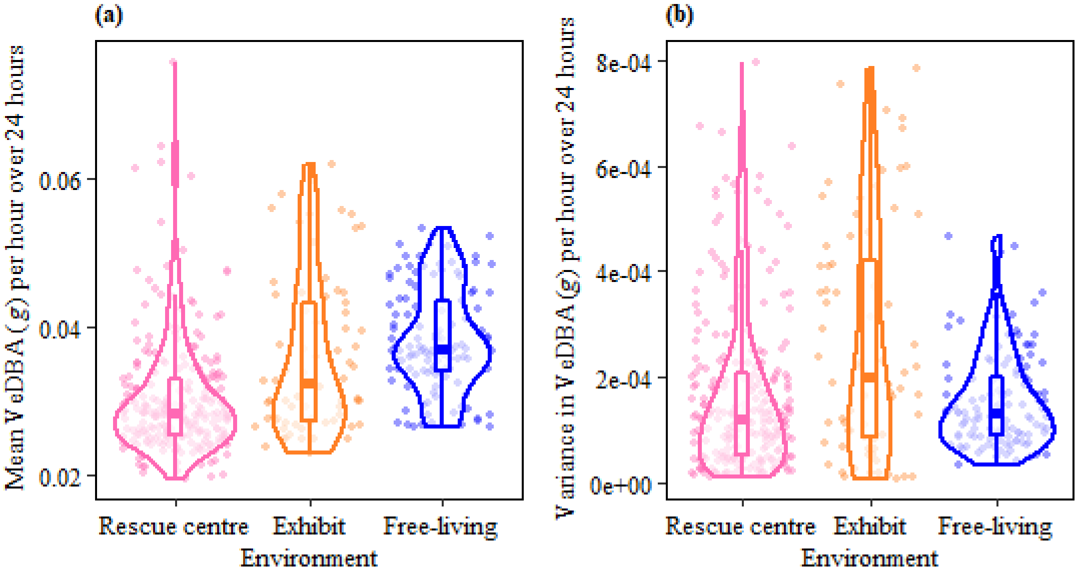


Figure 2. Activity data measured using VeDBA from turtles in tagged in rescue centre tanks (n = 10; depicted in pink), aquarium exhibits (n = 3; depicted in orange) and free-living turtles tagged in the wild (n = 5; depicted in blue). Violin plots show (a) the mean VeDBA per hour and (b) the variance in VeDBA per hour, during 24 hours of 'bottom time' added sequentially. The outline of the violin plot indicates point density and the boxplot within marks the lower, median and upper quartiles (corresponding to the 25%, 50%, and 75% quantiles respectively). Turtles in rescue centre tanks generally had lower mean VeDBAs than both exhibit and free-living turtles except for a few outliers. Similarly, the lowest VeDBA variance values per hour were recorded for turtles in tanks and exhibits although values were widely and relatively evenly spread, particularly in exhibits (note boxplot length). Despite this, neither VeDBA metric differed significantly with environmental setting (cf. Tables 3 and 4, GLMMs 1 and 2).

Table 3. Generalised linear mixed-effects models (GLMMs) with each family and link function specified. Models tested whether movement behaviours in turtles differed depending on whether they were free-living (the baseline point of reference), in rescue centre tanks or in aquarium exhibits. The AIC values were similar between each pair of null and full model, indicating minor differences in the goodness of model fit; models with significant differences between turtles in tanks and the wild had lower AICs indicating a better fit. All GLMM intercepts were highly significant, indicating that values were significantly different to zero (otherwise asterisks are used to indicate significance level: ‘’ 0.01; ‘**’ 0.001; ‘***’ 0.0001). The behaviour of turtles in tanks and exhibits was significantly different ($p < 0.05$) to that of free-living conspecifics for almost all movement metrics except those using VeDBA (GLMMs 1 and 2). Instead of t-values, z-values are presented for GLMMs 10–13 with Poisson error terms.*

GLMM	**AIC**	**Family**	**Link**	**Variable**		**Est.**	**S.E.**	***t*-value**	***p*-value**
Null 1	-3151.1	Gaussian	Log	Mean VeDBA	Intercept	-3.46	0.06	-57.82	< 0.0001
1	-3149.5				Intercept	-3.31	0.11	-30.76	< 0.0001
					Tank	-0.21	0.13	-1.64	0.101
					Exhibit	-0.11	0.17	-0.62	0.535
Null 2	-6880.2	Gamma	Log	VeDBA variance	Intercept	-8.82	0.16	-56.14	< 0.0001
2	-6876.8				Intercept	-8.81	0.29	-30.11	< 0.0001
					Tank	-0.08	0.36	-0.22	0.826
					Exhibit	0.26	0.49	0.54	0.587
Null 3	4528.2	Gamma	Log	Pitch variance	Intercept	4.34	0.15	28.21	< 0.0001
3	4522				Intercept	3.71	0.22	17.07	< 0.0001
					Tank	0.76	0.27	2.85	0.004**
					Exhibit	1.24	0.36	3.49	0.0005***
Null 4	1844.1	Gamma	Log	Pitch differential variance	Intercept	1.16	0.2	5.66	< 0.0001
4	1839.7				Intercept	0.31	0.31	1	0.317
					Tank	1.14	0.37	3.05	0.002**
					Exhibit	1.29	0.5	2.57	0.01*
Null 5	4128.8	Gamma	Log	Roll variance	Intercept	3.77	0.16	23.85	< 0.0001
5	4126.9				Intercept	3.22	0.25	12.63	< 0.0001
					Tank	0.73	0.31	2.33	0.020*
					Exhibit	0.92	0.42	2.22	0.026*
Null 6	1822.7	Gamma	Log	Roll differential variance	Intercept	1.07	0.2	5.3	< 0.0001
6	1818				Intercept	0.22	0.3	0.72	0.47
					Tank	1.17	0.37	3.17	0.002**

GLMM	AIC	Family	Link	Variable		Est.	S.E.	*t*-value	*p*-value
					Exhibit	1.22	0.49	2.48	0.013*
Null 7	8559	Gaussian	Log	Heading variance	Intercept	8.48	0.17	48.79	< 0.0001
7	8556.2				Intercept	8.9	0.27	23.61	< 0.0001
					Tank	-0.8	0.33	-2.38	0.017*
					Exhibit	0.09	0.45	0.2	0.843
Null 8	8903.3	Gamma	Log	Cumulative AAV	Intercept	9.51	0.14	65.83	< 0.0001
8	8893.9				Intercept	8.85	0.18	48.7	< 0.0001
					Tank	0.81	0.22	3.66	0.0003***
					Exhibit	1.24	0.3	4.19	< 0.0001***
Null 9	4351.4	Gamma	Log	AAV variance	Intercept	4.05	0.33	12.23	< 0.0001
9	4335.5				Intercept	2.28	0.36	6.32	< 0.0001
					Tank	2.24	0.44	5.06	< 0.0001***
					Exhibit	3.17	0.58	5.37	< 0.0001***
Null 10	18005	Poisson	Log	45° Turns	Intercept	4.29	0.2	21.7	< 0.0001
10	17992				Intercept	3.25	0.23	13.85	< 0.0001
					Tank	1.39	0.29	4.84	< 0.0001***
					Exhibit	1.66	0.38	4.34	< 0.0001***
Null 11	12812	Poisson	Log	90° Turns	Intercept	3.63	0.26	13.99	< 0.0001
11	12786				Intercept	2.03	0.21	9.59	< 0.0001
					Tank	2.15	0.26	8.33	< 0.0001***
					Exhibit	2.44	0.34	7.13	< 0.0001***
Null 12	5767.7	Poisson	Log	180° Turns	Intercept	2.34	0.33	7.03	< 0.0001
12	5744.5				Intercept	0.35	0.31	1.15	0.249
					Tank	2.59	0.37	6.98	< 0.0001***
					Exhibit	3.26	0.49	6.65	< 0.0001***
Null 13	1484.1	Poisson	Log	360° Turns	Intercept	-0.31	0.44	-0.71	0.478
13	1469.5				Intercept	-2.92	0.61	-4.77	< 0.0001
					Tank	3.41	0.71	4.84	< 0.0001***
					Exhibit	3.98	0.89	4.39	< 0.0001***

Continued.

Table 4. Post-hoc test results comparing the selected movement metrics for turtles in the wild vs tanks, wild vs exhibits and tanks vs exhibits; generalised linear mixed-effects model (*GLMM) numbering corresponds to that of Table 3. The behaviour of turtles in manage care, i.e., tanks and exhibits, did not differ significantly for any of the selected movement metrics. However, there were significant ($p < 0.05$) differences for comparisons with managed care environments against wild turtles for pitch variance, pitch and roll differential variance, cumulative AAV and AAV variance as well as all sampled turn extents. Asterisks denote significance: '*' 0.01; '**' 0.001; '***' 0.0001.*

GLMM	**Variable**	**Scenario comparison**	**Est.**	**S.E.**	***z*-value**	***p*-value**
1	Mean VeDBA	Wild *vs* tank	-0.21	0.13	-1.64	0.224
		Wild *vs* exhibit	-0.11	0.17	-0.62	0.806
		Tank *vs* exhibit	0.1	0.15	0.69	0.766
2	VeDBA variance	Wild *vs* tank	-0.08	0.36	-0.22	0.973
		Wild *vs* exhibit	0.26	0.48	0.54	0.848
		Tank *vs* exhibit	0.34	0.43	0.79	0.709
3	Pitch variance	Wild *vs* tank	0.76	0.27	2.85	0.012*
		Wild *vs* exhibit	1.24	0.36	3.49	0.001**
		Tank *vs* exhibit	0.48	0.32	1.5	0.286
4	Pitch differential variance	Wild *vs* tank	1.14	0.37	3.05	0.006**
		Wild *vs* exhibit	1.29	0.5	2.57	0.027*
		Tank *vs* exhibit	0.14	0.45	0.31	0.947
5	Roll variance	Wild *vs* tank	0.73	0.31	2.33	0.051
		Wild *vs* exhibit	0.92	0.42	2.22	0.067
		Tank *vs* exhibit	0.2	0.38	0.53	0.855
6	Roll differential variance	Wild *vs* tank	1.17	0.37	3.17	0.004**
		Wild *vs* exhibit	1.22	0.49	2.48	0.035*
		Tank *vs* exhibit	0.05	0.44	0.11	0.993
7	Heading variance	Wild *vs* tank	-0.8	0.33	-2.38	0.045*
		Wild *vs* exhibit	0.09	0.45	0.2	0.978
		Tank *vs* exhibit	0.88	0.4	2.2	0.07
8	Cumulative AAV	Wild *vs* tank	0.81	0.22	3.66	0.0006***
		Wild *vs* exhibit	1.24	0.3	4.19	< 0.0001***
		Tank *vs* exhibit	0.34	0.27	1.61	0.2401
9	AAV variance	Wild *vs* tank	2.24	0.44	5.06	< 0.0001***
		Wild *vs* exhibit	3.17	0.59	5.37	< 0.0001***

GLMM	Variable	Scenario comparison	Est.	S.E.	*z*-value	*p*-value
		Tank *vs* exhibit	0.93	0.53	1.75	0.184
10	45° Turns	Wild *vs* tank	1.39	0.29	4.84	< 0.0001***
		Wild *vs* exhibit	1.66	0.38	4.34	< 0.0001***
		Tank *vs* exhibit	0.27	0.34	0.78	0.711
11	90° Turns	Wild *vs* tank	2.15	0.26	8.33	< 0.0001***
		Wild *vs* exhibit	2.44	0.34	7.13	< 0.0001***
		Tank *vs* exhibit	0.3	0.31	0.96	0.599
12	180° Turns	Wild *vs* tank	2.59	0.37	6.98	< 0.0001***
		Wild *vs* exhibit	3.26	0.49	6.65	< 0.0001***
		Tank *vs* exhibit	0.67	0.44	1.54	0.271
13	360° Turns	Wild *vs* tank	3.41	0.7	4.84	< 0.0001***
		Wild *vs* exhibit	3.89	0.89	4.39	< 0.0001***
		Tank *vs* exhibit	0.48	0.73	0.65	0.788

Continued.

3.2 Pitch, roll and heading

Variance in pitch and roll (and their respective differentials) was generally greater among individuals in the two managed care groups, indicating greater angle changes across both axes. Values also covered a notably greater range showing greater inter-individual differences in movement behaviour (Figure 3). GLMM analysis revealed that pitch variance was significantly higher in tanks than in the wild (2.14 ± 1.31 times as high; Est. = 0.76 ± 0.27 (S.E), $t = 2.85$, $p = 0.004$; Table 3, GLMM 3) and significantly higher in exhibits than in the wild (3.46 ± 1.43 times as high; Est. = 1.24 ± 0.36 (S.E), $t = 3.49$, $p = 0.0005$; Table 3, GLMM 3). Post-hoc analysis found significant differences in pitch variance between wild *vs* tanks: $z = 2.85$, $p < 0.012$ and wild *vs* exhibits: $z = 3.49$, $p < 0.001$, but not between tanks *vs* exhibits (Table 4, GLMM 3).

The pitch differential variance was also higher in tanks than in the wild (4.22 ± 1.45 times as high; Est. = 1.44 ± 0.37 (S.E), $t = 3.05$, $p = 0.002$; Table 3, GLMM 4) and significantly higher in exhibits than in the wild (3.63 ± 1.65 times as high; Est. = 1.29 ± 0.5 (S.E), $t = 2.57$, $p = 0.01$; Table 3, GLMM 4). Further pairwise analysis revealed significant differences between wild *vs* tanks: z

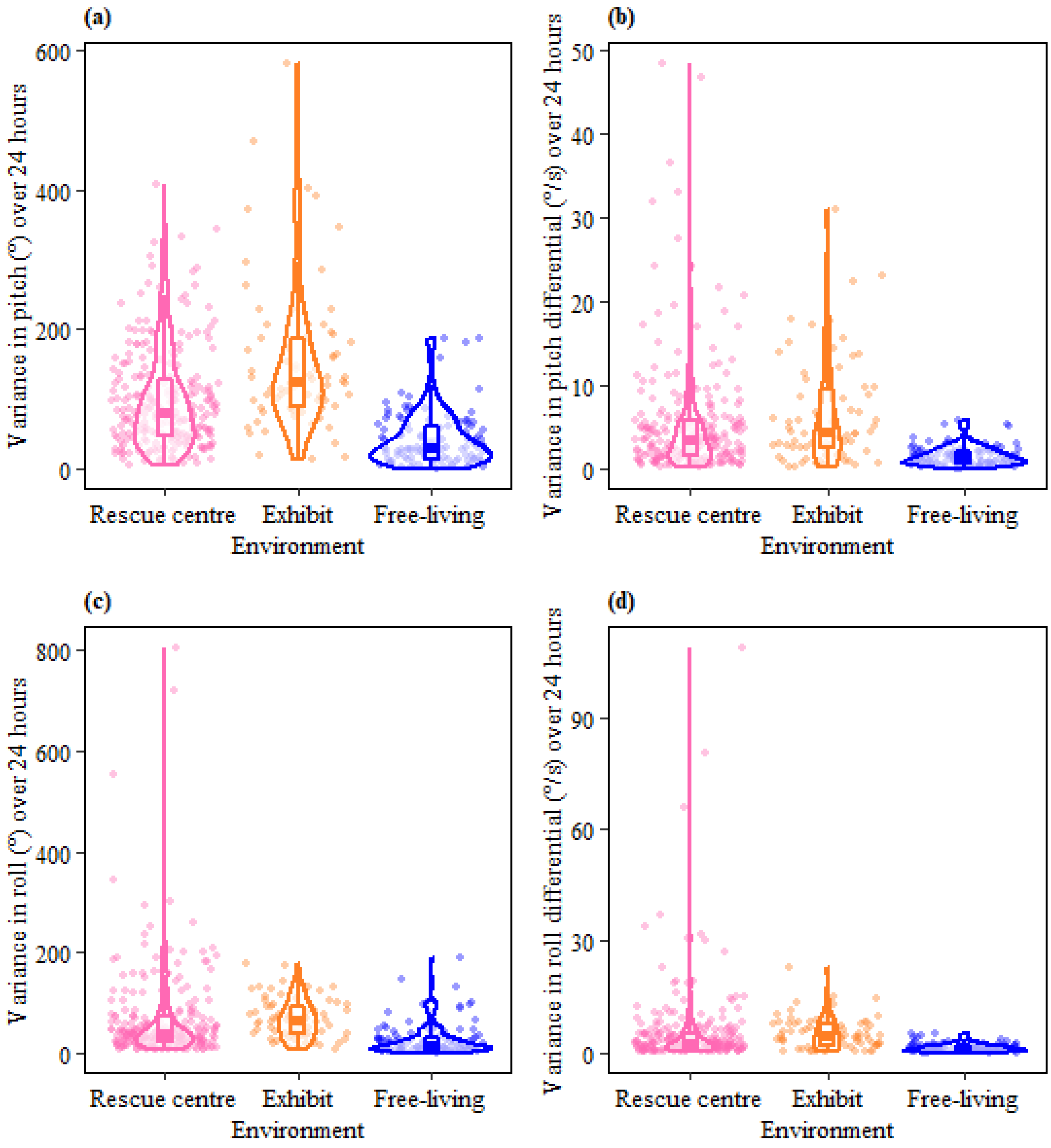


Figure 3. Pitch and roll data from turtles in tagged in rescue centre tanks (n = 10; depicted in pink), aquarium exhibits (n = 3; depicted in orange) and free-living turtles tagged in the wild (n = 5; depicted in blue). Violin plots show the variance in (a) pitch, (b) pitch differential, (c) roll and (d) roll differential, per hour over 24 hours of 'bottom time' data, added together from sequential U-shaped dives. The outline of the violin plot indicates point density and the boxplot within marks the lower, median and upper quartiles (corresponding to the 25%, 50%, and 75% quantiles respectively). Turtles in managed care (i.e., those in rescue centre tanks and exhibits; cf. Table 1) generally had higher values across all four measures of variance and a wider spread in values too. GLMMs revealed significant differences between rescue centre and free-living turtles for all four metrics (Table 3, GLMMs 3–6) and pairwise post-hoc comparisons revealed significant differences between both managed care scenarios and free-living turtles for all but roll variance (cf. Table 4, GLMMs 3–6).

=3.05, $p < 0.006$ and wild *vs* exhibits: $z = 2.57$, $p < 0.027$, but not between tanks *vs* exhibits (Table 4, GLMM 4). Although roll variance was found to be 2.08 ± 1.36 times higher in tanks than in the wild (Est. = 0.73 ± 0.31 (S.E), $t = 2.33$, $p = 0.02$; Table 3, GLMM 5) and 2.51 ± 1.52 times higher in exhibits than in wild turtles (Est. = 0.92 ± 0.42 (S.E), $t = 2.22$, $p = 0.026$ respectively; Table 3, GLMM 5), post-hoc pairwise comparisons were not significantly different (Table 4, GLMM 5). Similarly, the variance in the roll differential was significantly higher in tanks (3.22 ± 1.45 times higher; Est. = 1.17 ± 0.37 (S.E), $t = 3.17$, $p = 0.002$; Table 3, GLMM 6) and exhibits (3.39 ± 1.63 times higher; Est. = 1.22 ± 0.49 (S.E), $t = 2.48$, $p = 0.013$; Table 3, GLMM 6) when compared to the wild. Further analysis confirmed significant differences in wild *vs* tanks: $z = 3.17$, $p < 0.004$ and wild *vs* exhibits: $z = 2.48$, $p < 0.035$, but not for tanks *vs* exhibits (Table 4, GLMM 6).

Animals in exhibits and the wild demonstrated a higher variance in heading than most turtles in rescue centre tanks indicating greater rotational variation in more heterogenous environments (Figure 4). Similarly, statistical analysis revealed that when compared to free-living turtles, heading variance was significantly lower in rescue centre turtles (0.92 ± 1.39 times as high; Est. = -0.8 ± 0.33 (S.E), $t = -2.38$, $p = 0.045$) and significantly higher in exhibits (1.09 ± 1.57 times higher; Est. = 0.09 ± 0.45 (S.E), $t = 0.2$, $p = 0.843$). However post-hoc, pairwise comparisons only found a small significant difference between free-living and rescue centre turtles ($z = 2.38$, $p < 0.045$; Table 4, GLMM 7).

3.3 Angular movement

The AAV along with turn extents of 45°, 90°, 180° and 360° were calculated for each study animal over a 24-hour period. The AAV per hour and total number of turns per hour were both typically higher in both managed care scenarios, (especially exhibits) and lowest in the wild environment (Figures 5 and 6, respectively). Turtles in managed care attained significantly greater angular velocities than free-living turtles both in terms of cumulative AAV (rescue centre turtles were 2.25 ± 1.25 times higher; Est. = 0.81 ± 0.22 (S.E), $t = 3.66$, $p = 0.0003$; *and* exhibit turtles were 3.46 ± 1.35 times higher; Est. = 1.24 ± 0.3 (S.E), $t = 4.19$, $p < 0.0001$; Table 3, GLMM 8) and AAV variance (rescue centre turtles were 9.39 ± 1.55 times higher; Est. = 2.24 ± 0.44 (S.E), $t = 5.06$, p

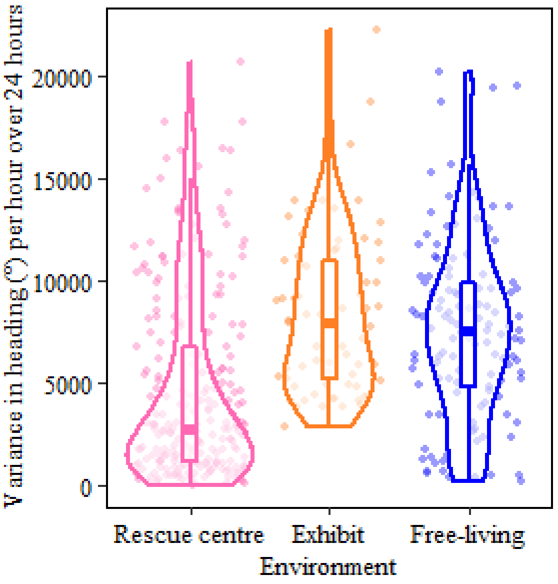


Figure 4. Heading (yaw) data from turtles in tagged in rescue centre tanks (n = 10; depicted in pink), aquarium exhibits (n = 3; depicted in orange) and free-living turtles tagged in the wild (n = 5; depicted in blue). Violin plots show the variance heading per hour over 24 hours of 'bottom time' data added together from sequential U-shaped dives. The outline of the violin plot indicates point density and the boxplot within marks the lower, median and upper quartiles (corresponding to the 25%, 50%, and 75% quantiles respectively). Turtles in rescue centre tanks (cf. Table 1) on average had comparably low heading variance, GLMM and post-hoc analysis, however, confirmed it was only significantly lower than free-living turtles (cf. Tables 3 and 4, GLMM 7).

= 0.0001; *and* exhibit turtles were 23.81 ± 1.78 times higher; Est. = 3.17 ± 0.58 (S.E), $t = 5.37$, $p < 0.0001$; Table 3, GLMM 9).

Post-hoc analysis for both cumulative AAV and AAV variance metrics revealed significant differences between wild *vs* tanks ($z = 3.66$, $p = 0.0006$ and $z = 5.06$, $p < 0.0001$ respectively; Table 4, GLMMs 8 and 9) and wild *vs* exhibits ($z = 4.19$, $p < 0.0001$ and $z = 5.37$, $p < 0.0001$ respectively; Table 4, GLMMs 8 and 9). As with the AAV metric, GLMMs revealed a highly significant (i.e., $p < 0.0001$) difference in the number of turns per hour between free-living turtles and those in tanks and exhibits. For turn extents of 45º, 90º, 180º and 360º, the number of turns completed by rescue centre turtles were 4.01 ± 1.34, 8.58 ± 1.3, 13.33 ± 1.45 and 30.27 ± 2.03

times higher respectively than wild turtles (Table 3, GLMMs 10–13). Exhibit turtles also had significantly higher turn rates than wild turtles (in order of sampled turn angles, smallest to highest: 5.26 ± 1.46, 11.47 ± 1.4, 26.05 ± 1.63 and 53.51 ± 2.44). Post-hoc pairwise comparisons also indicated significant differences between free-living and managed care turtle scenarios but not between tanks and exhibits (*cf.* Table 4, GLMMs 10–13).

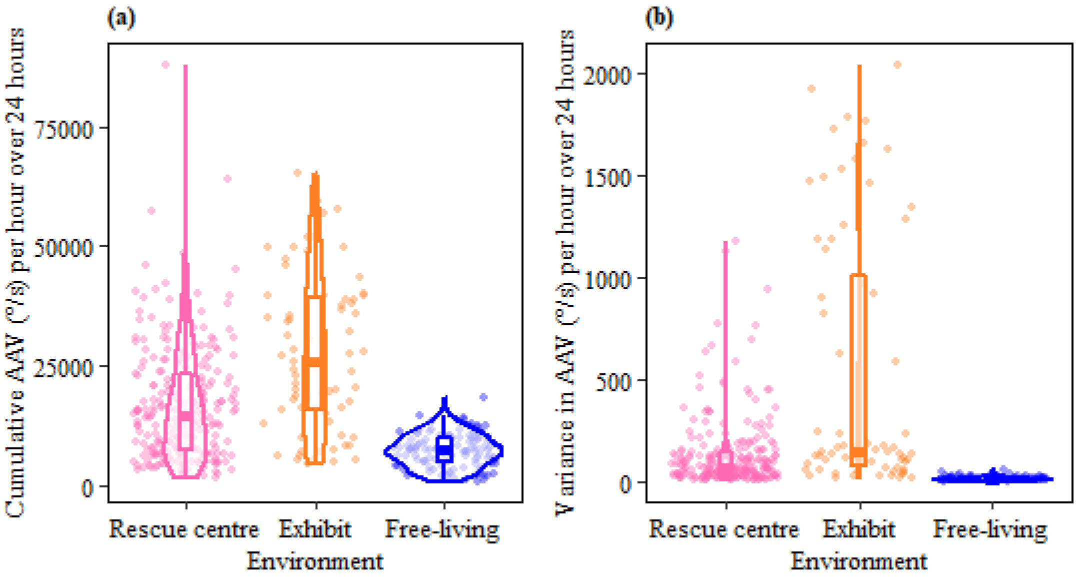


Figure 5. Absolute angular velocity (AAV) data from turtles in tagged in rescue centre tanks (n = 10; depicted in pink), aquarium exhibits (n = 3; depicted in orange) and free-living turtles tagged in the wild (n = 5; depicted in blue). Violin plots show the (a) cumulative AAV and (b) variance in AAV per hour, over 24 hours of 'bottom time' data added together from sequential U-shaped dives. The outline of the violin plot indicates point density and the boxplot within marks the lower, median and upper quartiles (corresponding to the 25%, 50%, and 75% quantiles respectively). Turtles in managed care (i.e., those in rescue centre tanks and exhibits; cf. Table 1) attained significantly greater angular velocities than turtles in the wild (cf. Tables 3 and 4, GLMMs 8 and 9).

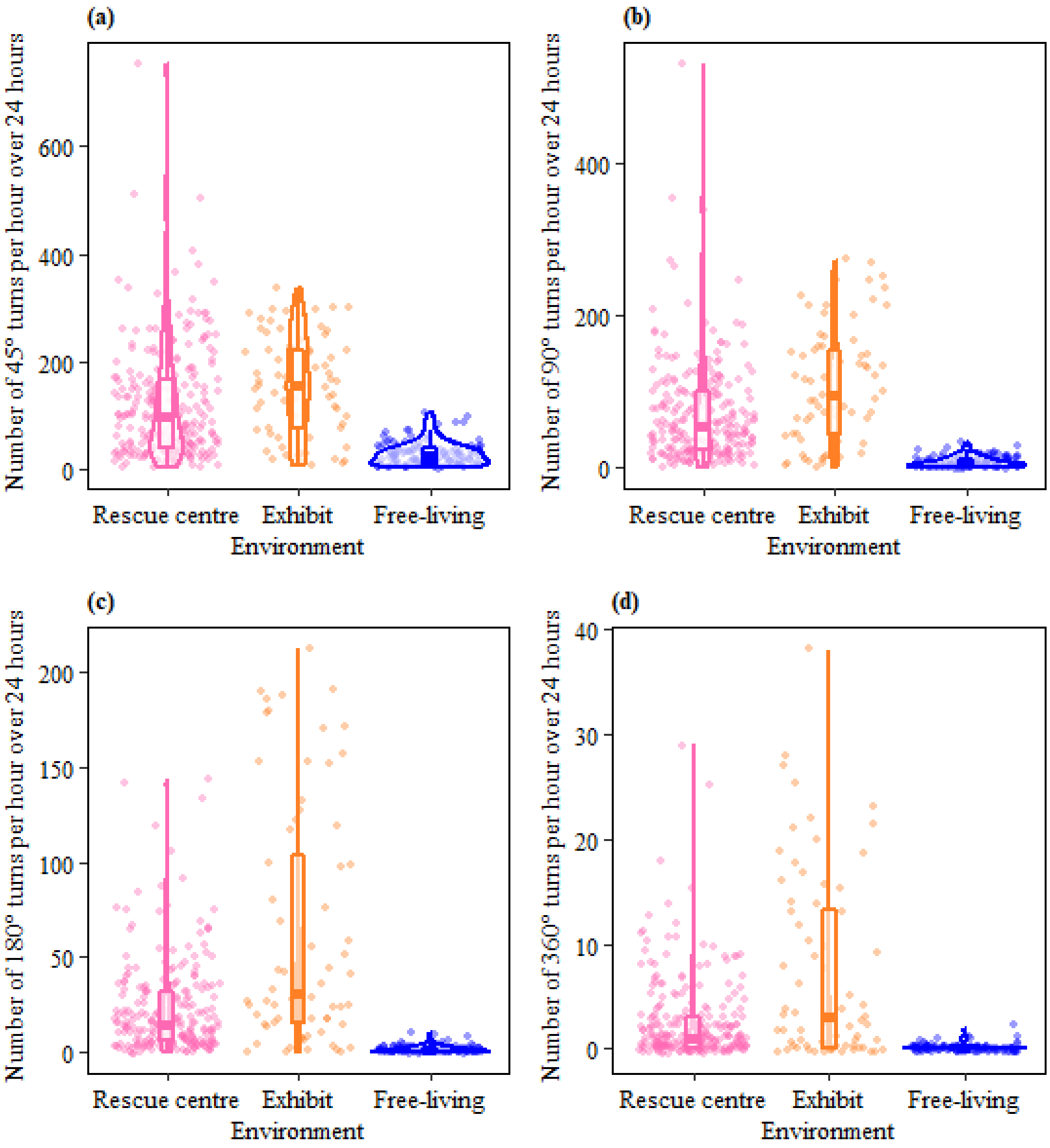


Figure 6. Total number of turns per hour over a 24-hour period for turtles in tagged in rescue centre tanks (n = 10; depicted in pink), aquarium exhibits (n = 3; depicted in orange) and free-living turtles tagged in the wild (n = 5; depicted in blue). Violin plots show the number of turns per hour that equalled or surpassed (a) 45°, (b) 90°, (c) 180° and (d) 360° during 24 hours of 'bottom time' data added together from sequential U-shaped dives. The outline of the violin plot indicates point density and the boxplot within marks the lower, median and upper quartiles (corresponding to the 25%, 50%, and 75% quantiles respectively). Turtles in managed care (i.e., those in rescue centre tanks and exhibits; cf. Table 1) had a significantly higher number of turns per hour than turtles in the wild for all sampled turn extents (cf. Tables 3 and 4, GLMMs 10–13).

4. Discussion

The attachment of multi-sensor tags to wild animals has been pivotal to our understanding of animal behaviour (Naito 2004; Brown et al. 2013), physiology (Block 2005; Sherub et al. 2017) and movement ecology (Ropert-Coudert & Wilson 2005; Nathan et al. 2008; Wilmers et al. 2015). The purpose of this study, however, was to tag sea turtles in managed care and compare their behaviour with free-living conspecifics. Given the marked differences between captive and wild environments, (particularly depth), data recorded during the 'bottom phase' of dives was selected for comparison. In brief, the findings in response to the three initial hypotheses were:

i. Activity, measured according to VeDBA, appeared to be lower on average in turtles housed in rescue centre tanks (when graphed), however, contrary to my expectations, differences in VeDBA between the three groups were not significant.

ii. The variance in heading was significantly higher in free-living turtles than turtles in rescue centre tanks (as expected given that turtles were regularly observed stationary and orientated towards water pipes or the central barriers of tanks), however, the variance in pitch and roll was generally higher in managed care turtles.

iii. Both the AAV and the total number of turns per hour were significantly higher in exhibit turtles than free-living turtles, supporting my initial hypothesis that turtles in more complex environments would exhibit increased rotation as a result of scanning their environment. However, turtles in barren rescue tanks also had a significantly higher AAV and turn rate than free-living turtles.

These findings are discussed at greater length in the following sections.

4.1 What can multi-sensor tags reveal about animal behaviour?

Despite obvious differences between managed care and wild environments, (primarily that animals in tanks had limited space whereas free-living animals had an almost unlimited 2-dimensional space and an extended 3-dimensional space in which to move), all study animals were able to perform U-shaped dive ‘bottom phase’ behaviours. Movement data during the bottom phase was selected in order to see how turtle behaviour compared between rescue centre tanks, aquarium exhibits and the wild.

4.1.1 VeDBA as a measure of activity

Turtles in tanks had limited room in which to move (2–6m diameter and 0.95m deep), making it impossible for them to swim quickly for any length of time without hitting the side of the tank. As such these individuals were expected to have much lower VeDBAs than both exhibit and free-living turtles; interestingly mean VeDBA and variance in VeDBA showed that this was not always the case as there was substantial overlap between the groups and statistical analysis found no significant differences between the three scenarios. The difference is perhaps not more clear-cut due to the sole use of bottom phase data from flat U-shaped dives which are characteristically known as ‘resting’ dives and thus unlike other dive types, are associated with energy conservation (Minamikawa et al. 1997; Hochscheid et al. 1999; Hays et al. 2000; Houghton et al. 2002). Another point to consider is that managed care and wild turtles were at different life stages which are typically associated with differing behaviours; the former group consisted of large juveniles (apart from two adults, Rosita and T234), that had been bycaught whilst foraging off the Valencian coast, whereas the latter group consisted of free-living, inter-nesting females, that were expected to reduce energy expenditure for egg maturation (Hays et al. 1999; Minamikawa et al. 2000; Houghton et al. 2002; Wallace et al. 2005). Thus, whilst there is some debate as to just how inactive inter-nesting females are (Hochscheid et al. 1999; Gunner et al. 2020), behavioural comparison may have been more valid between captive and wild turtles at the same life stage.

The use of acceleration data when quantifying animal activity is undoubtably useful (Brown et al. 2013; Wilmers et al. 2015) and measures of dynamic body acceleration, (such as VeDBA), are considered valid proxies for costs associated with movement and have consequently been used for a number of species including: molluscs, sea turtles, penguins, cormorants, auks, cheetahs, beavers and humans (see Wilson et al. 2006; Qasem et al. 2012; Wilson et al. 2020). When investigating links between energy expenditure and environment, it is however, important to recognize that movement metrics that are derived from acceleration data (like VeDBA) are as a consequence affected by water and air currents that can distort the signal-to-noise ratio (Halsey et al. 2011b). This reduces the reliability when assessing the behaviour of inactive, slow moving, and gliding animals that sustain near constant speeds for lengthy periods of time like sea turtles (Wyneken 1997; Eckert 2002) and soaring birds (Williams et al. 2015). For such species acceleration may often be negligible, making dynamic acceleration a poor metric for activity (Wilson et al. 2020). This may help explain why wild turtles tagged in this study did not have significantly higher VeDBAs than the managed care individuals.

4.1.2 Body orientation

Both free-living and exhibit turtles devoted less time to one orientation as expected, resulting in more varied rotational movement about the ‘y’ or yaw axis, (i.e., animal heading) than individuals in tanks (although there was only a significant difference between free-living *vs* tanks). In the wild, animals can generally travel a long distance before changing trajectory, as has been observed when using telemetry data to examine the distances between successively recorded positions– typically referred to as the step lengths (Patterson et al. 2017). Furthermore, an almost unlimited space enables animals moving in a direction to drift or change heading slowly over time without turning regularly. Individuals held in rescue centre tanks generally had the lowest variance in heading of the three groups; this may have resulted from a preference for a particular direction, like orientating their nose towards/against the filter pipe or some kind of stereotypic space use (*cf.* Mason & Latham 2004; Mason & Rushen 2008).

Confined spaces enclosed with vertical walls also have implications for movement metrics like pitch and roll (as well as turning, see section 4.1.3). For example, the variance in pitch and roll and their respective differentials was generally higher (and significantly so for all but roll variance) in managed care turtles than free-living turtles. The greatest variance in pitch was observed among exhibit turtles suggesting that the combination of increased depth and the high density of animals and structures in an enclosed space, resulted in sharp changes in pitch from navigating around obstacles. Interestingly the variance in both the pitch and roll differentials, (i.e., rate change) for wild turtles was lower than both turtles in tanks and exhibits, indicating that increased space and therefore time to alter movement direction, resulted in a lower rate change. The variance in roll for free-living and exhibit turtles was very much within the same range and both groups had no obvious outliers; turtles in tanks, however, often appeared to have a slightly higher roll variance and more outliers. These outliers could arise from irregular instances when turtles hit the edges of the tank and rolled beyond the limits of a standard range; nonetheless more outliers would be expected in the tank group because that is where most turtles were tagged. If encountering the tank wall leads to drastic changes in movement as suggested, I would also predict that the variance in pitch and roll (as well as their respective differentials) would decrease with increasing exhibit size and decreasing density of structures and other animals.

4.1.3 Angular velocity

Turtles maintained in rescue centre tanks were expected to have a lower AAV and to turn less than animals in environments with greater complexity (i.e., aquarium exhibits or the wild) where scanning behaviour of the environment was expected to increase rotation. However, this was not the case for free-living turtles which had significantly lower AAV and turn rate. From a logical point of view, a restricted area (like a small tank) is likely to result in not only slower movement, but also a need to turn more frequently upon encountering the tank wall. Upon reflection, turn frequency is likely to decrease with increasing enclosure size, especially if enclosures have a low density of objects or animals and there is no stimulus or obvious advantage to turning. The fact that the number of turns per hour was highest in exhibits, (although not significantly higher than tanks) would indicate that a complex 3D environment shared with other animals can augment turn rate and supports my hypothesis. Stereotypy may explain why turtles in both managed care environments had significantly higher turn rates than free-living conspecifics (*cf.* Brilot et al. 2009; Burghardt 2013; Rose et al. 2017b).

Examining scales of angular body rotation per unit time can elucidate movement patterns and activities that lack dynamism in body acceleration (Noda et al. 2012; Gunner et al. 2020) such as when animals are slow or gliding (Eckert 2002; Wilson et al. 2019). Furthermore, the collection of tri-axial accelerometry and tri-axial magnetometry data in unison, enables orientation about the yaw axis, i.e., animal heading, to be defined within about 1–2° (Painter et al. 2016; Gunner et al. 2021). With tri-axial magnetometry the orientation of the tagged animal is defined in respect to the Earth's magnetic field and postural angular rotation, ex. body rolls and flipper movements can be examined without interference from dynamic movement (Williams et al. 2017). The combination of heading and postural rotation (provided by tri-axial magnetometry) enhances the biological interpretation of data beyond that possible with tri-axial acceleration data alone (Williams et al. 2017; Gunner et al. 2021). For example examining rotational movements can reveal behaviours like foraging and circling, without the need for direct observation or video footage (Gunner et al. 2020). Findings relating to energetic costs are pertinent because all activity is energetically expensive (Wilson et al. 2020), with power costs rising with increasing angular extent and velocity (Wilson et al. 2013a), therefore quantifying activity during the inter-nesting period when turtles are expected to be conserving energy (Omeyer et al. 2017), could help understand power and energy management.

4.2 Limitations and perspectives

Whilst this study showcases the potential for motion- and orientation sensitive tags in a managed care setting as well as the wild, there are obvious limitations, namely a lack of study animals, especially in exhibits and in the wild. Attaining an adequate sample size for biologically or statistically significant results is challenging; wild animals are often cryptic and inhabit environments that are not easily accessed by humans, i.e., in aquatic, arboreal and aerial realms (Shepard et al. 2008b; Wilson et al. 2008; Whitney et al. 2010; Brown et al. 2013) and the number of individuals kept in managed care is usually small (Swaisgood & Shepherdson 2005; Kuhar 2006). For this study all of the turtles in managed care (except Rosita) were tagged opportunistically (an added challenge) following admission to the rehabilitation centre and a veterinary assessment to check that they were free from signs of disease or injury or that they had recovered.

Ideally a greater sample size and longer tag attachment durations or repeated measures of the same individuals in different settings, would be necessary to give proper statistical credibility to these initial findings. Despite this, statistical analysis did indicate significant changes in behaviour in terms of pitch, heading, AAV, and the number of turns per hour depending on environment. These environment-induced behavioural changes suggest that the use of tags for captive *versus* wild behavioural comparisons could be instrumental in creating optimal captive environments. The application of multi-sensor tags could be made even more convenient, especially in wild environments, *via* remote data collection in real time (Laske et al. 2014; Wilmers et al. 2015) both reducing animal handling and speeding up data analysis.

As mentioned previously, behavioural comparisons may have been more meaningful if tagged turtles had been at the same life stage; when it comes to tagging turtles in the wild, nearly all studies have tagged nesting females (Hays et al. 2001; Godley et al. 2002; Houghton et al. 2002; Rees et al. 2008; Zbinden et al. 2008; Hamann et al. 2010) from which tags can be relatively easily deployed and retrieved. Not having compared like with like does mean that the observed differences in behaviour could be a product of environment, life stage or both. Inter-individual differences in size, carapace slope and sensor inclination may also affect signal input and movement sensor recordings (Gunner et al. 2020) resulting minor offsets in baseline pitch and roll values could not be corrected for because turtles did not remain still after tagging; because of this I analysed variance instead of variable means. Despite the limitations considered here, the cultural and economic worth of animals in zoos and aquariums does mean that even rudimentary data is considerably better than nothing when endeavouring to improve animal well-being in captivity.

4.3 Future directions

Aside from egg-laying females, few studies have attempted to tag either males or indeed other turtle life-stages in the wild, such as foraging juveniles, which for this study would have been a more suitable comparison. Another gap in current data is tagging animals in managed care, including turtles; valuable data like how effective rehabilitation is, could also be garnered from tagging animals upon release. Although it might not make sense or be beneficial for captive animals to display the same behavioural repertoire as wild conspecifics, understanding the behavioural plasticity that already exists in the wild may help improve the quality of life for animals in captivity and formulate husbandry guidelines to reduce detrimental stereotyped behaviours. Furthermore, if desired, knowledge on wild and captive animal repertoires could potentially be used to create environments that encourage certain wild-type behaviours. Fortuitously, plenty of suitable data may already exist as logging devices have been widely deployed on wild animals over the last few decades (Eckert 2002) and could be compared with animals tagged in zoos and aquariums in order to define a set of expected behavioural states and/or activity levels. Many of the issues related to animal well-being in captive care (see Rose et al. 2017a; Rose et al. 2017b; Shorter et al. 2017), including, stress and stereotypic behaviours, could potentially be well quantified by animal-attached devices.

5. Conclusion

This chapter presents data collected from motion- and orientation-sensitive tags and demonstrates how derived movement metrics could be used to provide insight into differences between captive and wild animal behavioural repertoires in a quantifiable and robust manner. Specifically, the ‘bottom’ phase of dives recorded for free-living and managed care turtles in different environmental settings, were compared to see if and how their behaviour differed. Although VeDBA did not differ significantly between the scenarios, turtles in managed care environments were found to have a significantly higher pitch variance, pitch differential variance, roll differential variance, heading variance, cumulative AAV, AAV variance and number of turns per hour than free-living turtles. I believe that this is occurred because (i) turtles in exhibits with 3D structures and other animals turned in order to navigate around obstacles and scan their environment, and (ii) turtles in rescue centre tanks could not swim far before reaching the side of a tank and needing to turn. Collecting behavioural information, (as this study has), for various species housed in zoos and aquariums could help staff create environments that elicit desired behaviours or levels of activity, whether they are of a wild-type nature or not. Considering that the maintenance of animals in captivity (particularly large mammals and other vertebrates) is frequently under scrutiny (Keulartz 2015), objective measures of well-being would prove valuable husbandry tools.

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Chapter 6

Towards informed animal enclosure size; a ‘Realisable Movement Index’

Abstract

Delivering a high standard of animal care is a top priority for zoos and aquariums around the world. Zoological associations often provide animal husbandry guidance and set standards which their member institutions must follow in order to be accredited. Guidance typically concerns appropriate nutrition, environmental stimuli and opportunities for behavioural expression and is often based on what has worked in captive care previously. A plausible next step for further enhancing captive environments may be to apply our understanding of free-living animal movement patterns in consideration of enclosure size. Today, high-resolution movement data from multi-sensor tags details animal movement paths, elucidating straight-line distances travelled (step lengths) and turning points.

Using high-resolution movement path data from nine free-living species (aquatic species: Imperial cormorant, *Leucocarbo atriceps*; loggerhead, *Caretta caretta*; Magellanic penguin, *Spheniscus magellanicus*; whale shark, *Rhincodon typus*; terrestrial species: Aldabra giant tortoise, *Aldabrachelys gigantea*; Arabian oryx, *Oryx leucoryx*; domestic sheep, *Ovis aries*; European badger, *Meles meles meles* and volant species: Andean condor, *Vultur gryphus*), this study quantified step length distributions and examined how they related to existing zoo enclosures and enclosure size guidelines via a ‘Realisable Movement Index’, *ReMI*.’ In essence *ReMI* is a measure of the percentage of step lengths that can be accommodated within the longest dimensions of a given enclosure. Generally the percentage of step lengths accommodated was low– for six out of nine species studied, less than 3 % of step lengths could be realised within existing enclosure guidelines. Animals with relatively short step lengths fared better, for example guidelines for Aldabra giant tortoise and loggerhead turtles permitted over 60% of their natural step lengths. The implications of maintaining animals in enclosures that permit varying degrees of free-living movement are discussed. Given that a number of the animal care manuals and husbandry sources

reviewed provided little or even no guidance on enclosure size, *ReMI* (or a similar framework) could be used to help inform enclosure size and maximise animal well-being in captivity.

1. Introduction

The attachment of multi-sensor tags to wild animals has transformed our understanding of wild animal movement ecology (Ropert-Coudert & Wilson 2005; Nathan et al. 2008; Wilmers et al. 2015), behaviour (Naito 2004; Whitney et al. 2010; Brown et al. 2013; Whitney et al. 2016) and physiology (Block 2005; Sherub et al. 2017). Importantly, an understanding of animal movement, an important aspect of behaviour, gives researchers powerful insights into effective conservation (Wilson et al. 2008; Bograd et al. 2010; Wilson et al. 2015), as well as species-specific behaviours and requirements (Ropert-Coudert & Wilson 2005; Shepard et al. 2008; Wilson et al. 2008; Fossette et al. 2010; Brown et al. 2013; Wilson et al. 2017).

In the past, the study of drivers of animal movement using global positioning systems (GPS), and Argos telemetry, collected relatively low-resolution data, with intervals between datapoints ranging from several minutes to hours (Johnson et al. 2002; Jerde & Visscher 2005; Hurford 2009; McClintock et al. 2015; Hays et al. 2021). Recent technological advancements in animal tags, however, especially those using accelerometers and magnetometers (Wilson et al. 2008; Brown et al. 2013; Noda et al. 2014; Bidder et al. 2015; Walker et al. 2015; Williams et al. 2017), have enabled animal movement paths to be studied in detail, elucidating periods of straight-line travel and discrete turn-points with sub-second resolution (Potts et al. 2018).

Such ultra-high-resolution data, where the intervals between data points are smaller than the time it would take an animal to move their own body length, generate movement paths that can be considered continuous (Wilmers et al. 2015). This means that such data can be examined with respect to ‘steps and turns’, a concept for studying movement paths that has been central to the field of movement ecology for decades (Kareiva & Shigesada 1983; Bovet & Benhamou 1988; Turchin et al. 1991; Turchin 1998). However, this approach, which has involved a variety of methods, including step selection analysis, biased correlated random walks (Codling et al. 2008), state-space models, and continuous-time models (Parton et al. 2016), has generally had to work with relatively poorly resolved data, both in space and/or time. In this, a ‘step length’ is typically defined as the distance between two consecutively recorded GPS locations (Jerde & Visscher 2005). Two consecutive points are required to estimate distance and speed while three consecutive points are required to estimate a turn angle (Jerde & Visscher 2005).

Importantly within high-resolution, continuous movement path data, a step length can be defined as the distance travelled before changing direction (Potts et al. 2018). Turn-points indicate a decision to change direction instead of just continuing a straight-line trajectory (Potts et al. 2018), with animals changing direction in response to resource distribution, obstacles (e.g., bodies of water, rocks and vegetation), topography, social interactions and predators (Hampson et al. 2010a; Shepard et al. 2013; Aini et al. 2015; Richardson et al. 2018).

Capitalising on high resolution movement path data, already available from deployments of multi-sensor tags (Daily Diaries, DDs (Wilson et al. 2008); Wildbyte Technologies Ltd., Swansea, UK) on free-living animals, I propose a novel framework, incorporating step length, i.e., the distance travelled before changing direction, into a ‘Realisable Movement Index’, *ReMI*. This compares the frequency distribution of the step lengths of wild animals with the maximum dimensions of the captive animal enclosures, effectively defining the proportion of movement steps that can be carried out by captive animals compared to their wild counterparts. For this, step lengths from free-living animals were compared against recommended enclosure guidelines and existing enclosure sizes at various zoos and aquariums for a variety of aerial, terrestrial and aquatic animals. This approach should show the extent to which captive conditions adhere to those experienced by wild animals, highlighting inter-specific differences and perhaps making a case for modified enclosure size guidelines.

1.1 Background on zoo and aquarium husbandry

Zoos and aquariums adhere to detailed husbandry care manuals set out by various zoological associations (see Table 1). These associations have certain animal welfare standards that must be met for member zoos and aquariums to be accredited: for example, the Association for Zoos and Aquariums (AZA) states that all animal enclosures must be of a size and complexity sufficient to provide for the animal's physical, social, and psychological well-being (Accreditation Standard 10.3.3). Similarly, members of the European Association for Zoos and Aquariums (EAZA) are expected to provide species in their care with a high standard of accommodation that takes into account space requirements, social needs, appropriate management by staff and how to appropriately display animals to the public (EAZA 2014; 2020). In addition, natural behavioural repertoires should be encouraged through a mixture of enclosure design, enrichment and feeding regimes (EAZA 2014; 2020). However, many existing manuals do not provide guidance on minimum enclosure sizes (see: Gilbert & Woodfine 2004; AZA Wild Pig, Peccary and Hippo TAG 2008; Smith et al. 2004; 2017; AZA Pelecaniformes TAG 2012; Náhlik et al. 2017; De Kock et al. 2018; EAZA Tapir and Suiform TAG 2018; AZA Rodent, Insectivore and Lagomorph TAG 2021) and when guidelines are included they are sometimes based on existing enclosure sizes (Higgins 2002; AZA Raptor TAG 2010; AZA Charadriiformes TAG 2014) rather than a scientific framework that takes into account a given species needs.

2. Methodology

2.1 Daily diary deployments

Motion- and orientation-sensitive tags, DDs, (Wilson et al. 2008), were put on a number of aerial, terrestrial and aquatic species at different locations for varying deployment lengths (Table 2). All DDs recorded tri-axial acceleration, tri-axial magnetic field strength, ambient temperature and pressure (Wilson et al. 2008). Acceleration was recorded within a range of ± 16 *g* and magnetic field strength recorded with 0.73 mG/LSb resolution (range ± 0.88 G). Both acceleration and magnetic field strength were recorded along three orthogonal axes matching the dorso-ventral, lateral, and anterior-posterior axes of the animal (Williams et al. 2017). The tags recorded between 20–40 Hz and always weighed less than 3 % of the animals' body weight (Table 2).

Table 1. Information regarding the zoological associations mentioned within this manuscript, including a brief synopsis of what each association does, their mission(s), the number of member facilities and the estimated visitors per year when available, as well as each associations website address. All associations mentioned are members of the World Association of Zoos and Aquariums, WAZA. For more information, including a comprehensive list of all 23 association members visit the WAZA website.

Association; Abbreviation	***Synopsis***	***Mission(s)***	***No. of members and visitors***	***Website***
Association of Zoos and Aquariums; AZA	Founded in 1924. AZA-accredited zoos and aquariums meet the highest standards in animal care and welfare and provide a fun, safe, and educational family experience.	To advance zoos and aquariums in the areas of conservation, education, science, and recreation.	235+ facilities in the US and overseas receiving over 200 million visitors per year.	https://www.aza.org/
British and Irish Association of Zoos and Aquariums; BIAZA	Founded in 1966. BIAZA is the professional body representing the best zoos and aquariums in the UK and Ireland. BIAZA and its members are dedicated to conserving the natural world through research and conservation programmes whilst educating and inspiring visitors to do the same.	To inspire people to conserve the natural world; to participate in effective conservation; to deliver high quality education and research; to achieve the highest standards of animal welfare in zoos and the wild.	100+ facilities in the UK and Ireland receiving over 35 million people per year.	https://biaza.org.uk/
Central Zoo Authority; CZA	Founded in 1992. The body of the government of India responsible for oversight of zoos, formed to bring Indian zoos up to international standards. The CZAs role is to complement and strengthen national efforts regarding the conservation of local biodiversity.	To provide better upkeep and veterinary care to wild animals housed in Indian zoos to ensure their conservation through best management practises whilst bringing education and awareness to visitors.	145 recognised facilities (368 derecognised facilities).	https://cza.nic.in/
European Association of Zoos and Aquaria; EAZA	Founded in 1992. EAZA ensures that member zoos and aquariums achieve and maintain the highest standards of care and breeding for the species they keep empowering European citizens to learn about and contribute to global biodiversity conservation goals.	To facilitate cooperation within the European zoo and aquarium community towards the goals of education, research, and conservation.	340+ facilities in the EU and the Middle East receiving over 140 million visitors per year.	https://www.eaza.net/

Association; Abbreviation	***Synopsis***	***Mission(s)***	***No. of members and visitors***	***Website***
World Association of Zoos and Aquariums; WAZA	Founded in 1935. The global alliance of regional associations, national federations, zoos and aquariums, dedicated to the care and conservation of animals and their habitats around the world. WAZA promotes cooperation between zoos, aquariums, national and regional associations, wildlife experts, academies, and universities.	To guide, encourage and support the zoos, aquariums and like-minded organisations of the world in animal care and welfare, environmental education and global conservation.	400+ facilities from around the world.	https://www.waza.org/

Continued.

**All association websites were accessed on 13.05.22.*

2.2 Determining step length

High-resolution data, collected *via* orientation- and motion-sensitive tags (DDs) provides information that can be used to determine animal heading during travel (Gunner et al. 2021). From this, straight-line sections of the movement paths (i.e., step lengths– *SL*) and turning-points (TP) can be identified using an algorithm devised by Potts et al. (2018). This algorithm slides a window over a time-series of animal headings, searching for spikes in the squared circular standard deviation (SCSD). The SCSD is a measure of the ‘spread’ of angles and is used instead of variance in order to allow for the circular nature of angular distributions (i.e., that 0° = 360°). Spikes in the SCSD indicate changes in the direction of animal movement and potential TPs in the data.

A spike in a time-series of SCSDs is registered when the values in a sequence of data points are greater than the mean of the dataset (Figure 1). The mid-point of each spike is then collected, forming a subset of potential TPs which are then refined further by eliminating those with turn angles that are below a given threshold, thus leaving a set of inferred TPs. This process enables the algorithm to correct against noise arising from animal movement (such as the small rocking caused by an animal’s gait), as well as the inherent error in data-gathering technologies. A threshold of 30° was used in line with the simulations carried out by Potts et al. (2018). Thus, a TP was registered, and a step length was set to terminate each time a turn exceeded 30°.

Table 2. Details of tag deployments on study animals. In some cases, tag weight as a percentage of body weight was not calculated, however it never exceeded 3 %.

Species, Latin name	***No.***	***Location***	***Date***	***Deployment length (days)***	***Sampling frequency (Hz)***	***Tag weight as % of body weight***	***Reference***
				(Volant species)			
Andean condor, Vultur gryphus	4	Bariloche, Argentina	2013–2018	≤ 10	40	< 1	(Williams et al. 2020)
				(Terrestrial species)			
Aldabra giant tortoise, Aldabrachelys gigantea	3	Round Island	May–Jun 2016	12	20	< 3	(Redcliffe 2016)
Arabian oryx, Oryx leucoryx	7	Mahazat as-Sayd, Saudi Arabia	Aug 2014–Feb 2015	10	40	0.88	(Wilson et al. 2021a)
Domestic sheep, Ovis aries	3	Patagonia, Argentina	2014	1	40	< 2	(Wilson et al. 2018)
European badger, Meles meles meles	5	Northern Ireland	2015–2017	~10	40	2.97	(Wilson et al. 2021a)
				(Aquatic species)			
Imperial cormorant, Leucocarbo atriceps	5	Punta Leon, Argentina	Nov 2017	1–2 (one foraging trip)	25	1.1–1.4	(Gómez-Laich et al. 2022)
Loggerhead turtle, Caretta caretta	5	Boa Vista, Cape Verde Islands	Jul–Aug 2014	~14 (one inter-nesting interval)	40	< 3	(Gunner et al. 2020)
Magellanic penguin, Spheniscus magellanicus	5	San Lorenzo, Argentina	Nov–Dec 2019	1–2 (one foraging trip)	40	< 1	(Gunner et al. 2021)
Whale shark, Rhincodon typus	5	Ningaloo Reef, Australia	Feb–July 2020	> 1	20	< 1	Norman et al. unpublished

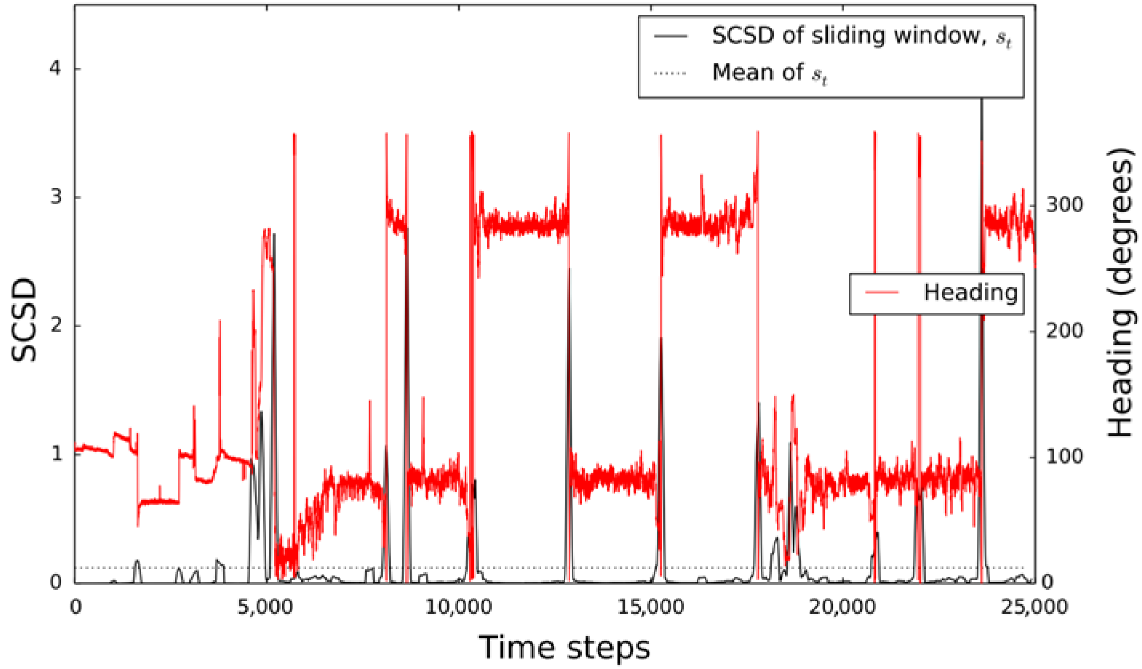

Figure 1. Depiction of how turning points (TPs) were determined using the squared circular standard deviation (SCSD). The red line shows a sample of recorded headings from an oryx, measured at 40 Hz. The black line shows the SCSD of the heading over a sliding window of 200 data points, where this spikes above the mean SCSD (dotted line), a potential TP is registered and then accepted if the change in heading reaches a given threshold, i.e., an angle of 30°. Extracted from Potts et al. (2018).

2.3 Enclosure size data

Initially I began contacting zoos and aquariums *via* email, asking if they would be willing to share enclosure size measurements anonymously for the purpose of this study. The 'Zootierliste' webpage, https://www.zootierliste.de/en/, and websites of zoos and aquariums were used to gather information on which species were maintained at each facility. Participating institutions were asked to measure the enclosure sizes of selected species currently (or previously) housed in their exhibits if blueprints or diagrams with enclosure size information did not exist. Facilities were asked to provide the enclosure length and width in metres as well as the shape (i.e., whether rectangular, oval or a trapezium). If unable to provide length and width measurements, zoos were asked for the enclosure area (m^2). Using simple trigonometry, this information was used to estimate longest straight-line path that could be undertaken within a given enclosure. In some cases, longest straight-line path could be provided by the participating institution.

Emails were sent to a total of 132 facilities around the world between the dates 13.09.21–26.10.21; of these, 118 emails were sent to zoos in Europe (41 of which were located in the UK), six were sent to zoos in the US and the remaining eight zoos were located in Asia. After it became apparent that a high percentage of zoos required a research proposal in order to participate, emails were sent with a generic research proposal attached (see Appendix I for a sample email and proposal). Initially zoos were asked to provide enclosure size data on 26 different species (see Appendix I, generic research proposal) but due to time constraints only nine species were included in this chapter (as such, some of the zoos that responded with enclosure sizes were not included). Following advice from a number of zoos within the UK, I contacted BIAZA to see if they would write a letter of support for the project: member zoos prioritise research topics considered to be of greatest importance by the associations of which they form part. Emails were also sent to AZA and EAZA for the same reason.

Meanwhile, Google Scholar was used to search for animal care manuals with recommended enclosure guidelines for the desired species in order to increase the sample size of enclosure data. Minimum space requirements were obtained from manuals published by AZA and CZA as well as government livestock guidelines and animal husbandry books. No recommended enclosure size guidelines were found for whale sharks, consequently the tank dimensions provided were taken from the Elasmobranch Husbandry Manual (Smith et al. 2004; 2017).

Enclosure size guidelines were used to calculate the longest path of straight-line travel permitted within an enclosure not taking into account any potential obstacles. Often guidelines provided a minimum recommended area rather than specific length and width dimensions, in such cases the longest length of straight-line travel was estimated for rectangular shaped enclosures (as they are the most common) of the specified area; all rectangles were twice as long as they were wide (measurements for length, width and height/ depth are provided in Appendix J). For example, the CZA minimum enclosure space recommendation for a pair of Aldabra giant tortoises was an area of 200 m^2, thus, a 10 x 20 m rectangular enclosure would allow a maximum straight-line travel of 22.4 m.

2.4 Analysis

2.4.1 Step length distances

The step length durations from all individuals for each study species were multiplied by mean travel speeds (Table 3), to give step length distance, before being pooled and converted into percentage frequencies and cumulative frequencies to allow straightforward visual comparisons between step length and enclosure size. Mean travel speeds were used because animals typically move in a way that maximises distance and minimises metabolic energy expenditure so as to travel at their most efficient speed that gives them the minimum cost of transport (Wilson et al. 2021b). Step length distance graphs were then constructed in R-Studio (version 3.6.0, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project. org/), using the R package 'ggplot2' (Wickham 2016).

2.4.2 *ReMI* calculations and application

Next, the estimated longest length of enclosures (Table 4) was divided by the step length distance at two distinct points in the cumulative frequency distribution of step lengths (at the 50 % and 90 % limits). This process generated two values that were indicative of the proportion of step lengths that could be realised within a given enclosure size and was used to create the Realisable Movement Index, '*ReMI*'.

These two points were taken at the 50 % and 90 % limits of the cumulative frequency distribution in order to distinguish between and highlight which species had relatively long or short step length distances and in consequence give an idea of ranging behaviour. Further, taking the 90 % limit removed potential outliers at the upper extreme of that data which may have resulted from irregular movements, such as if an animal was travelling along a straight road or a barrier of some sort (*cf.*

Clevenger et al. 2001; Dell'Ariccia et al. 2008; Asensio et al. 2009; Loarie et al. 2009). In addition, the 50 % limit served as a useful measure of half-way and added context, especially because some species covered very long step length distances and a number of existing zoo enclosures and size guidelines were orders of magnitude lower than the 90 % limit. To differentiate the 50 % and 90 % limits from other step lengths they were termed critical step lengths and denoted '$CSL_{50\%}$' and '$CSL_{90\%}$', respectively.

Table 3. Summary of mean travel speeds that were used in calculations of step length distance (±SD or minimum and maximum values in parentheses given when available), study locations and respective references.

Species, Latin name	***Mean speed (m/s)***	***Location(s)***	***Reference***
(Aerial species)			
Andean condor, Vultur gryphus	9.1 (max 13.56)	Bariloche, Argentina	(Williams et al. 2020)
(Terrestrial species)			
Aldabra giant tortoise, Aldabrachelys gigantea	0.07* (max 0.17)	Santa Cruz Island, Galápagos	(Rodhouse et al. 1975)
Arabian oryx, Oryx leucoryx	0.83 (max 1.9)	Bakgalagadi Schwelle, Botswana	(Boyers et al. 2021)
Domestic sheep, Ovis aries	1.06 ± 0.19	NA (study used pressure sensing walkway)	(Kim & Breur 2008)
European badger, Meles meles meles	0.25 (0.08–0.56)	Białowieża Primeval Forest, Poland	(Kowalczyk et al. 2006)
(Aquatic species)			
Imperial cormorant, Leucocarbo atriceps	1.15 (0.8–1.5)	Caleta Malaspina & Punta León, Argentina	(Quintana et al. 2007)
Loggerhead turtle, Caretta caretta	0.5 ± 0.1	Sanriku, northern Pacific coast of Japan	(Narazaki et al. 2013)
Magellanic penguin, Spheniscus magellanicus	1.77 ± 0.40	San Lorenzo, Punta Loberia, San Julian, Cabo Virgenes & New Island, Argentina	(Wilson et al. 2002)
Whale shark, Rhincodon typus	0.53 (0.33–0.89)	Ningaloo Reef, northern Western Australia	(Sleeman et al. 2010)

**Walking speeds are taken from the Galapagos tortoise, another species of giant tortoise similar to the Aldabra giant tortoise.*

If the longest length of an enclosure and the '$CSL_{90\%}$' were equal (for example if they were both 50 m), $ReMI_{CSL\_90\%}$ would equal 1 (because 50 ÷ 50 = 1). Thus, a $ReMI_{CSL\_90\%} = 1$ equated to an enclosure accommodating up to 90 % of step lengths if the animal travelled up the longest length of the enclosure.

For this study, a $ReMI_{CSL\_90\%} \geq 0.9$ was considered 'suitable' (this equated to allowing 90 % of 90 % which equals 81 % of total step lengths). Ergo the minimum 'suitable' enclosure size permitted at least 81 % of the total step lengths (which translated to a minimum enclosure length of 45 m if the $CSL_{90\%}$ was 50 m). A $ReMI_{CSL\_90\%} \geq 0.5$ was considered 'adequate' (this equated to allowing 50 % of 90 % which equals 45 % of total step lengths) and below this was considered 'undersized'. For comparison and to highlight differences between the two *CSL* thresholds, I also presented *ReMI* values using the $CSL_{50\%}$, where a $ReMI_{CSL\_50\%} \geq 1$ was considered 'adequate', and values below were considered 'undersized' (N.B. other potentially viable thresholds and movement behaviours on which *ReMI* could be based are reviewed in the discussion).

3. Results

3.1 Enclosure size data

Of the 132 zoos and aquariums contacted via email, a total of 50 facilities replied (27 in Europe, 19 in the UK, two in the US, one in the UAE and one in Taiwan), 14 of which were willing to participate and sent enclosure size data (six in Europe, six in the UK, one in the UAE and one in Taiwan). Eight of the 14 participating zoos and aquariums that provided enclosure sizes for species that were included in this study have been assigned a letter (for example 'Zoo A' or 'Aquarium A') for anonymity. Zoo B provided enclosure measurements for three different species, Zoos A and D provided two, and Zoos C, E, F provided one, as did Aquariums A and B. Contacted zoo associations, AZA and EAZA did not respond to application emails and BIAZA declined to lend their support.

3.2 Step length data

Step length data is presented for all nine study species, including step length distances at 50 % and 90 % with their respective $ReMI_{CSL\_50\%}$ and $ReMI_{CSL\_90\%}$ scores (Table 4). For all animals except Andean condors and whale sharks (which had higher *CSL* values), the $CSL_{50\%}$ fell within a 19–72 m range; the $CSL_{90\%}$ was much more varied, ranging from 43–277 m. According to my definitions, Aldabra giant tortoises and loggerhead turtles were the only animals with 'adequate' enclosure size guidelines ($ReMI_{CSL\_50\%}$ = 1.2 and $ReMI_{CSL\_90\%}$ = 0.55, respectively). All volant, terrestrial and aquatic animals were graphed together, highlighting differences in step length frequencies and cumulative frequencies (Figure 2). For example, Andean condors and whale sharks covered comparably long step length distances at 90 % (12,647 m and 1,676 m, respectively) whilst loggerhead turtles, Aldabra giant tortoise and Arabian oryx covered relatively short ones (≤ 65 m). Study animals were also graphed individually, showing the frequency and the cumulative frequency of step length distances for all volant (Figure 3), terrestrial (Figures 4–7) and aquatic animals (Figures 8–11) with shaded areas corresponding to the step length distance permitted by a given enclosure or size guideline.

In no cases did guidelines or enclosure sizes (even the largest ones) permit 100 % of recorded step length distances for any study animal. In fact, for a number of animals, recommendations were frequently below the smallest recorded step length distance (Andean condors, Figure 3; domestic sheep, Figure 6; imperial cormorants, Figure 8 and Magellanic penguins, Figure 10). Existing enclosure sizes always exceeded recommendations, however no existing enclosure size data was obtained for Andean condors, imperial cormorants or Magellanic penguins. Even when guidelines only permitted less than 5 % of step lengths (as they did for Arabian oryx, domestic sheep and European badgers; Figures 5, 6 and 7, respectively), zoo enclosure sizes typically accommodated at least 30% or more.

The highest percentage of realisable movement found was for Arabian oryx (Figure 5) housed in a large zoo enclosure for 49 animals that allowed 98.8 % of step length distances. In contrast, minimum requirements set by the AZA Antelope TAG (2001) permitted only 1–2.3 % of their step lengths. Considerable differences between association space guidelines and existing enclosure

Table 4. Care manuals providing enclosure size guidelines for the nine species used in this study. The recommended length x width x height or depth of enclosures (see Appendix J for details) was used to estimate the longest length of straight-line travel that they permitted. If care manuals only gave a recommended enclosure area, longest lengths were calculated within rectangular shaped enclosures (twice as long as they were wide) of the recommended area. Abbreviations for enclosure types are as follows: 'min', minimum enclosure size guidelines; 'max', the largest enclosure size recorded during exhibit surveys; 'sing.', 'pair', 'trio' and 'flock', minimum guidelines for a single animal, a pair, a trio and a flock of animals and 'mix', guidelines for a mixed species enclosure (see Table notes for explanations of enclosures and remaining abbreviations). Last, the longest length of enclosures was divided by critical step length distances at 50% and 90% limits in the frequency distributions of step lengths ($CSL_{50\%}$ and $CSL_{90\%}$ respectively) to generate two ReMI values (shaded grey). $ReMI_{CSL\_50\%}$ values (lighter grey) that were ≥ 1 and $ReMI_{CSL\_90\%}$ values (darker grey) that were ≥ 0.5 were considered 'adequate' and are in **bold**.

Species, Latin name	**Care manual**	**Enclosure type**	**Longest length (m)**	**$CSL_{50\%}$**	**$CSL_{90\%}$**	**ReMI $_{CSL\_50\%}$**	**ReMI $_{CSL\_90\%}$**
(Aerial species)							
Andean condor, *Vultur gryphus*	AZA Raptor TAG, 2010, *Andean Condor Care Manual*	*[1]Min	19.8	1834	12647	0.01	< 0.01
		Max	39.1			0.02	< 0.01
	CZA Zoos in India, 2014, *Legislation, Policy, Guidelines and Strategy (flying birds)*	*[2]Sing.	14.2			0.01	< 0.01
		Mix.	27.4			0.01	< 0.01
		Walk-thr.	223.6			0.12	0.02
(Terrestrial species)							
Aldabra giant tortoise, *Aldabrachelys gigantea*	CZA Zoos in India, 2014, *Legislation, Policy, Guidelines and Strategy (Aldabra giant tortoise)*	*[3]Min	22.4	19	51	**1.2**	0.4
Arabian oryx, *Oryx leucoryx*	AZA Antelope TAG, 2001, *Antelope, Alcelaphinae Husbandry Manual*	*[4]Sing.	11.9	30	65	0.4	0.2
		Pair	13.6			0.5	0.2
Domestic sheep, *Ovis aries*	CZA Zoos in India, 2014, *Legislation, Policy, Guidelines and Strategy (wild sheep)*	*[5]Min	35.3	49	85	0.72	0.41

Species, Latin name	***Care manual***	***Enclosure type***	***Longest length (m)***	$CSL_{50\%}$	$CSL_{90\%}$	***ReMI*** $CSL\_50\%$	***ReMI*** $CSL\_90\%$
	Welsh Assembly Government, 2010, *Code of Practice for the Welfare of Livestock: Sheep* NFACC, 2013, *Code of Practice for the Care and Handling of Sheep*	*[6]Trio Flock	3.3 13.2			0.07 0.27	0.04 0.16
European badger, *Meles meles meles*	AZA Small Carnivore TAG, 2010, *Mustelid, Mustelidae Care Manual*	*[7]Min	8.6	40	277	0.21	0.03
(Aquatic species)							
Imperial cormorant, *Leucocarbo atriceps*	CZA Zoos in India, 2014, *Legislation, Policy, Guidelines and Strategy*	*[8]Mix.	12.3	50	131	0.25	0.09
Loggerhead turtle, *Caretta caretta*	Higgins BM, 2002. Sea turtle husbandry. Pages 411-440. *The Biology of Sea Turtles, Volume II*	*[9]A B C	18.9 23.6 22.7	19	43	0.99 **1.24** **1.19**	0.44 **0.55** **0.53**
Magellanic penguin, *Spheniscus magellanicus*	AZA Penguin TAG, 2014, *Penguin (Spheniscidae) Care Manual*	*[10]Min	2.8	72	182	0.04	0.02
Whale shark, *Rhincodon typus*	Smith et al. 2004. *The Elasmobranch Husbandry Manual: Captive Care of Sharks, Rays and Their Relatives*	*[11]OEA	29.5	131	1,676	0.23	0.02
	Smith et al. 2017. *The Elasmobranch Husbandry Manual II: Recent Advances in the Care of Sharks, Rays and Their Relatives*	*[11]AA GA OAK OCA	76.2 84.2 34 44.2			0.58 0.64 0.26 0.34	0.05 0.05 0.02 0.03

Continued.

*[1] *Longest length calculated from minimum guidelines based off average enclosure sizes in North America collected during the 2007–2008 AZA Andean Condor SSP exhibit survey; the maximum corresponded to the largest enclosure recorded.*

*[2] *Longest length calculated for aviaries housing flying/water birds of a single and mixed species; minimum recommended areas were 80 m² and 300 m² respectively. Values were also given for a walk-through aviary 'walk-thr.', with a minimum recommended width of 100 m and an area of 20,000 m².*

*[3] *Longest length based on the recommended area for a breeding pair (200 m²).*

*[4] *Longest length values correspond to those advised for a single animal and a pair, based on recommended areas 56 m^2 and 74 m^2 respectively.*

*[5] *Longest length based on the recommended outdoor enclosure area for a single animal, (500 m^2 per individual; guidelines recommend adding 100 m^2 for each animal after that).*

*[6] *Longest length based on pen measurements for a trio of animals (the minimum advised as sheep are highly sociable) and a flock of 50 animals (the maximum advised). Values were based on minimum floor requirements of 1.4 m^2 per ewe, yielding an area 4.2 m^2 for the trio and 70 m^2 for the flock.*

*[7] *Longest length based on recommendations for housing 1–2 badgers with head to body lengths of 81.3 cm.*

*[8] *Longest length calculated for water bodies within aviaries housing water birds of mixed species; the minimum recommended area of water was 60 m^2 within a 300 m^2 enclosure, however, it was also recommended that 50% of the area be covered by water.*

*[9] *Longest length calculated for two of the larger sea turtle pens (labelled 'A' and 'B') at the National Marine Fisheries Service Panama City (NMFSPC) facility with areas of 142 m^2 and 223 m^2 respectively; pen 'A' housed 10–30 turtles weighing 5–25 kg and pen 'B' housed up to 200 turtles weighing 7 kg (2 years old). Sea turtles weighing 5–25 kg were stocked at densities of 4.2–4.7 m^2 per turtle; sea turtles weighing 90–200 kg (adults) were stocked at 4–6.5 m^2 per turtle. Longest length was also calculated for a pond ('C') at the Cayman Turtle Farm (CTF) with an area of 207 m^2 and a volume of 289.8 m^3.*

*[10] *Longest length based on pool guidelines for a minimum of ten penguins (terrestrial guidelines were not included as step lengths were taken from swimming penguins); minimum requirements for pool and land areas were 3.2 m^2 and 5.8 m^2 respectively.*

*[11] *Longest lengths based on reported tank sizes. Abbreviations denote aquariums with whale sharks and are as follows (respective locations and tank volumes also given): Okinawa Expo Aquarium, 'OEA', Japan, ~1,134 m^3 (increased to 7,500 m^3 as of 2002 but no measurements were given); Atlantis Aquarium, 'AA', UAE, 11,000 m^3; Georgia Aquarium, 'GA', USA, 15,300 m^3; Osaka Aquarium Kaiyukan, 'OAK', Japan, 5,400 m^3; Okinawa Churaumi Aquarium, 'OCA' Japan, 7,500 m^3. All tanks house a variety of fish species, including whale sharks and other large elasmobranchs. The manual gave no recommended enclosure sizes for whale sharks.*

sizes also existed for European badgers: AZA Small Carnivore TAG (2010) guidelines allowed for 2.8 % of recorded step lengths to be undertaken whereas two reported enclosure sizes were sufficiently big enough to accommodate 36.5–44.3 % of straight-line travel. Guidelines for Aldabra giant tortoises set by CZA, (2014; Figure 4) were the most generous, permitting up to 61.9 % of step lengths and reported zoo enclosures exceeded this, allowing up to 87.1 %. Similarly, head-starting facility dimensions for loggerhead turtles (Figure 9), as reported by Higgins (2002), permitted between 48.5–62.8 % while a mixed species tank at an aquarium accommodated 98 % of straight-line travel. In contrast, enclosure sizes and guidelines for animals with the longest step lengths, Andean condors and whale sharks (Figures 3 and 11), only accounted for 0.9 % and 36.4 % respectively of step lengths at best.

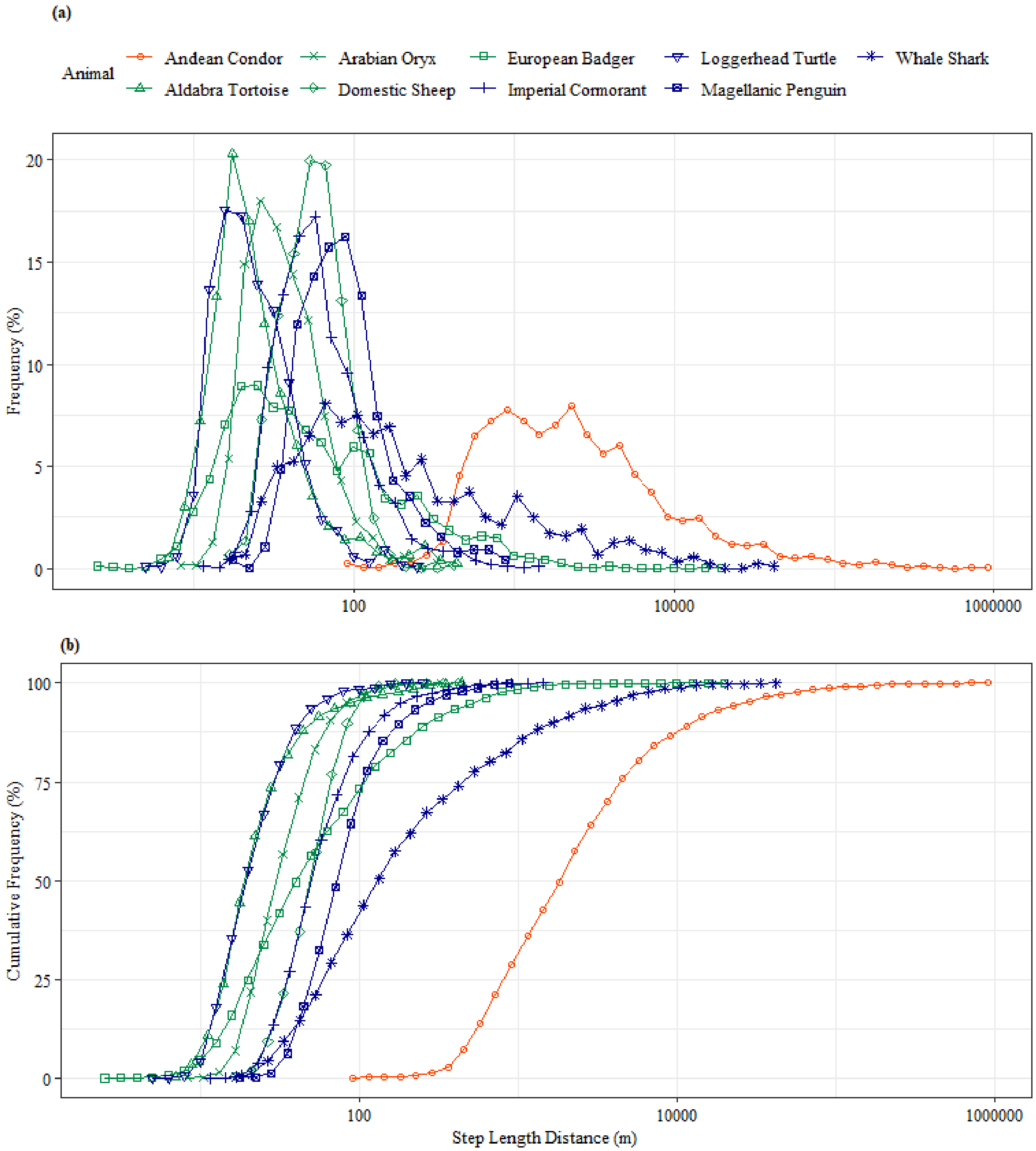

Figure 2. Step length distance data for a variety of aerial, terrestrial and aquatic animals (depicted in orange, green and blue, respectively; see legend) showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths. Distances are displayed on the log scale in order to present all animals on one graph. Note that the loggerhead turtle and the Aldabra giant tortoise travelled the shortest straight-line distances with a CSL$_{90\%}$ (critical step length at the 90 % limit of the cumulative frequency distribution) of 43 m and 51 m, respectively. The Andean condor had the longest CSL$_{90\%}$ (12,647 m), followed by the whale shark and the European badger (1,676 m and 277 m, respectively).

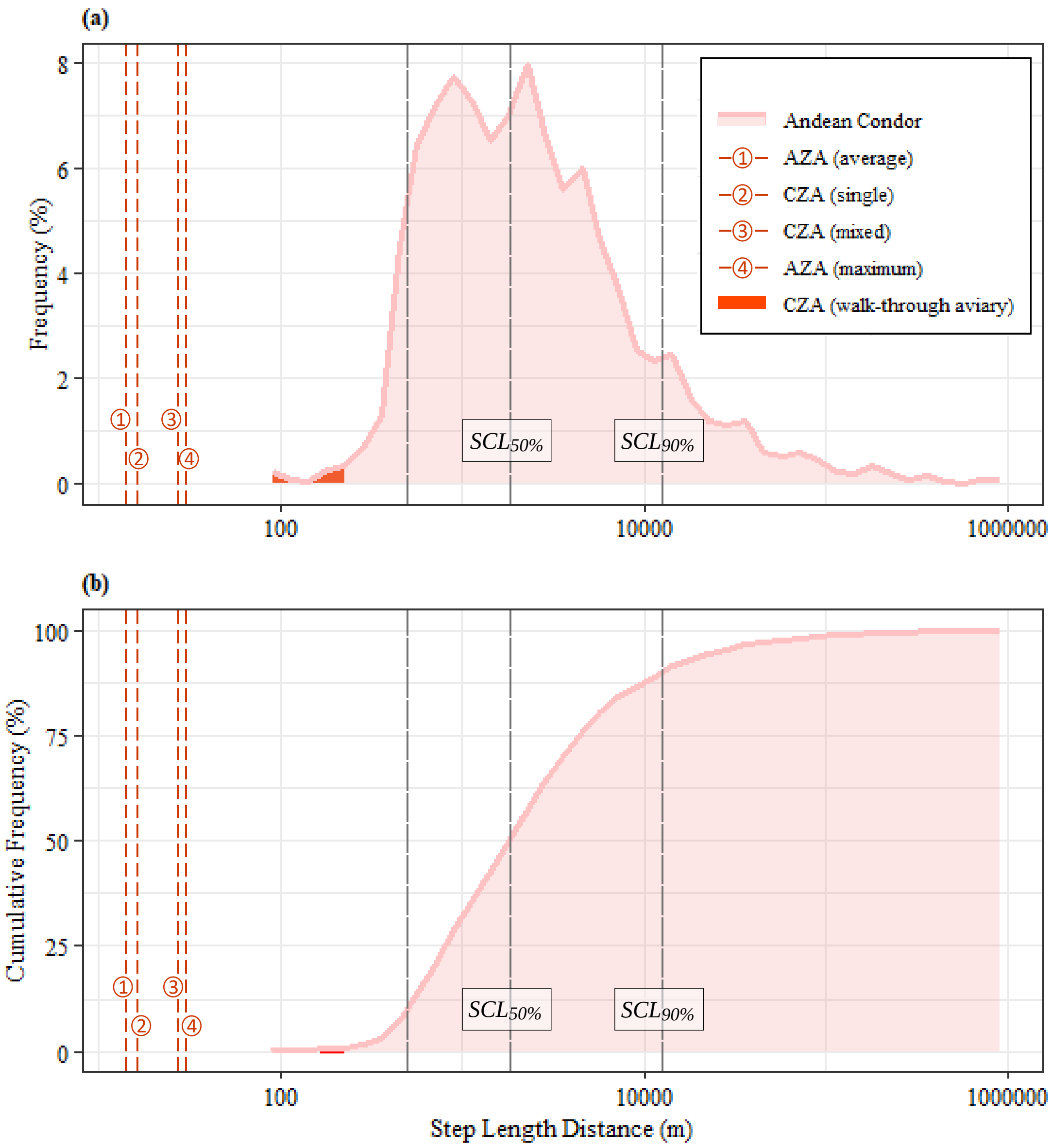

Figure 3. Step length distance data from four Andean condors showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths (m). Average and maximum enclosure lengths of zoos in the US, as reported by the AZA Raptor TAG (2010) and CZA (2014) guidelines for single and mixed species enclosures (vertical red dotted lines 1–4; see Table 4) were below the shortest step lengths recorded (meaning that they would fail to permit even 0.2 % of distances travelled); the CZA guidelines for a walk-through aviary were somewhat larger (cf. Table 4), but still only permitted 0.9 % of step length distances. The vertical grey lines indicate where cumulative frequencies of 10 %, 50 % (CSL$_{50\%}$) and 90 % (CSL$_{90\%}$) fall in the data and correspond to step length distances of 504 m, 1,834 m and 12,647 m, respectively. The highest frequencies of step length peaked first around 900 m and again around 2,300 m. N.B. Step length distance (m) is presented on the log scale, hence the proportion of step lengths permitted within enclosures will appear greater than it is.

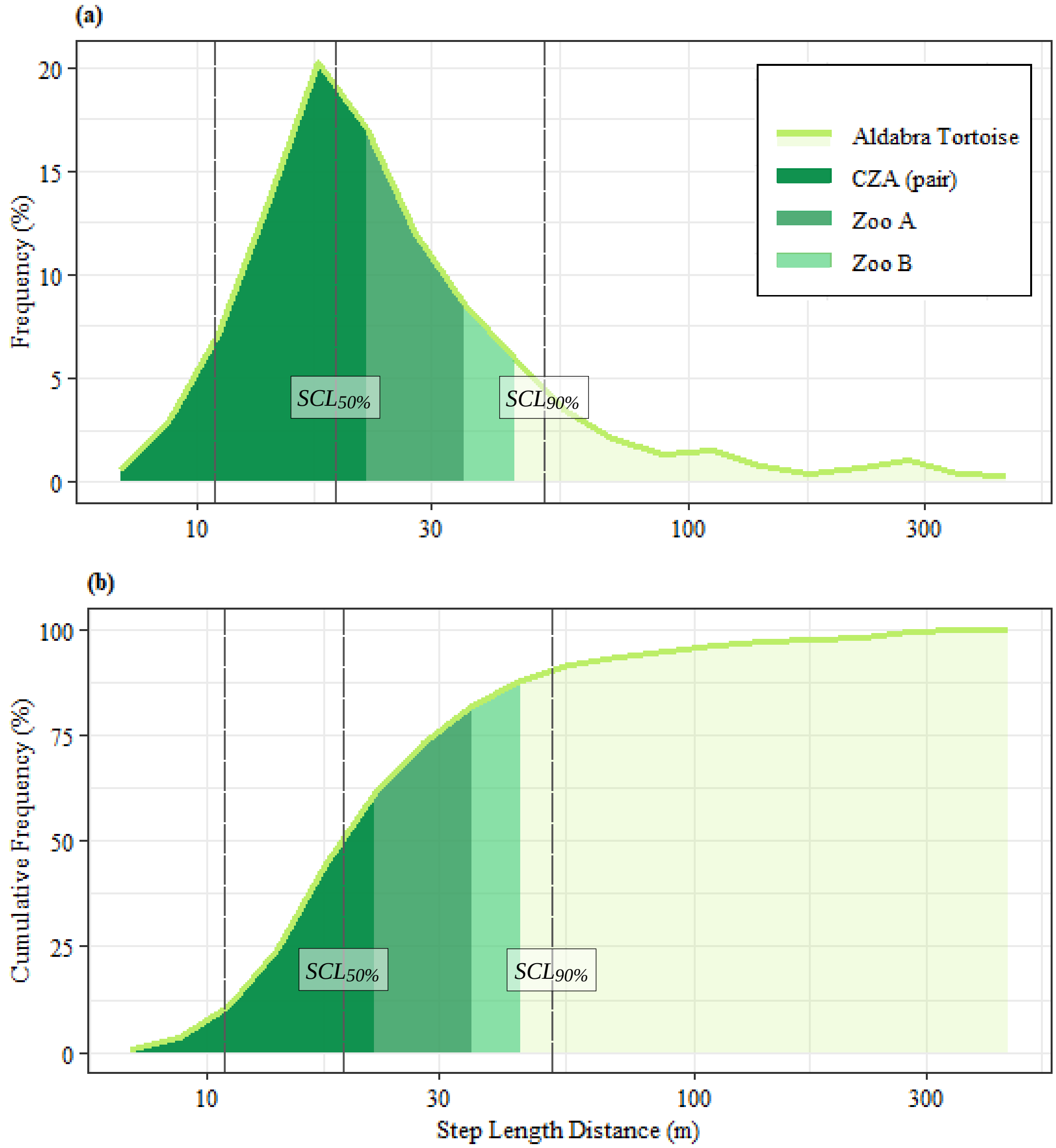

Figure 4. Step length distance data from three Aldabra giant tortoises showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths (m). The vertical grey lines indicate where cumulative frequencies of 10 %, 50 % ($CSL_{50\%}$) and 90% ($CSL_{90\%}$) fall in the data and correspond to step lengths of 11 m, 19 m and 51 m respectively; the highest frequencies observed occurred around the 18 m mark. Guidelines for a pair of tortoises as set out by CZA (2014) giving 22.4 m, permitted up to 61.9 % of step lengths; Zoo A (33 m) and Zoo B (41.6 m) allowed 79.9 % and 87.1 % respectively. N.B. Step length distance (m) is presented on the log scale, hence the proportion of step lengths permitted within enclosures will appear greater than it is.

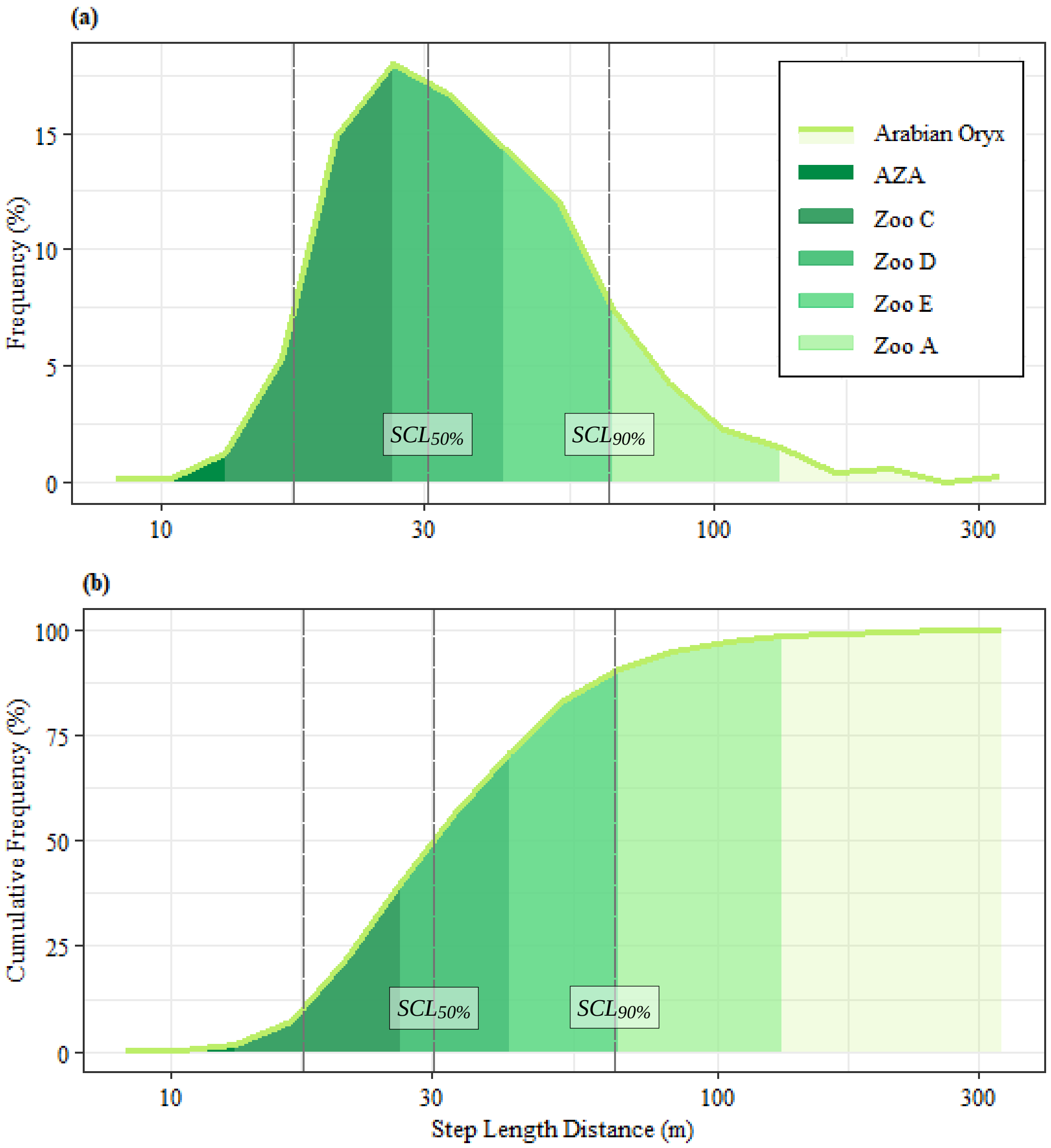

Figure 5. Step length distance data from seven Arabian oryx showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths (m). The vertical grey lines indicate where cumulative frequencies of 10 %, 50 % (CSL$_{50\%}$) and 90 % (CSL$_{90\%}$) fall in the data and correspond to step lengths of 17 m, 30 m and 65 m, respectively. Step length distances ranging between 26–33 m were most frequent; these exceeded minimum AZA Antelope TAG (2001) requirements for housing oryx both individually (11.9 m) and in pairs (13.6 m) which only allowed 1–2.3 % of step lengths. All reported zoo enclosures (which ranged from 25.6–143 m) greatly exceeded AZA requirements, permitting 38.7–98.8 % of step lengths. N.B. Step length distance (m) is presented on the log scale, hence the proportion of step lengths permitted within enclosures will appear greater than it is.

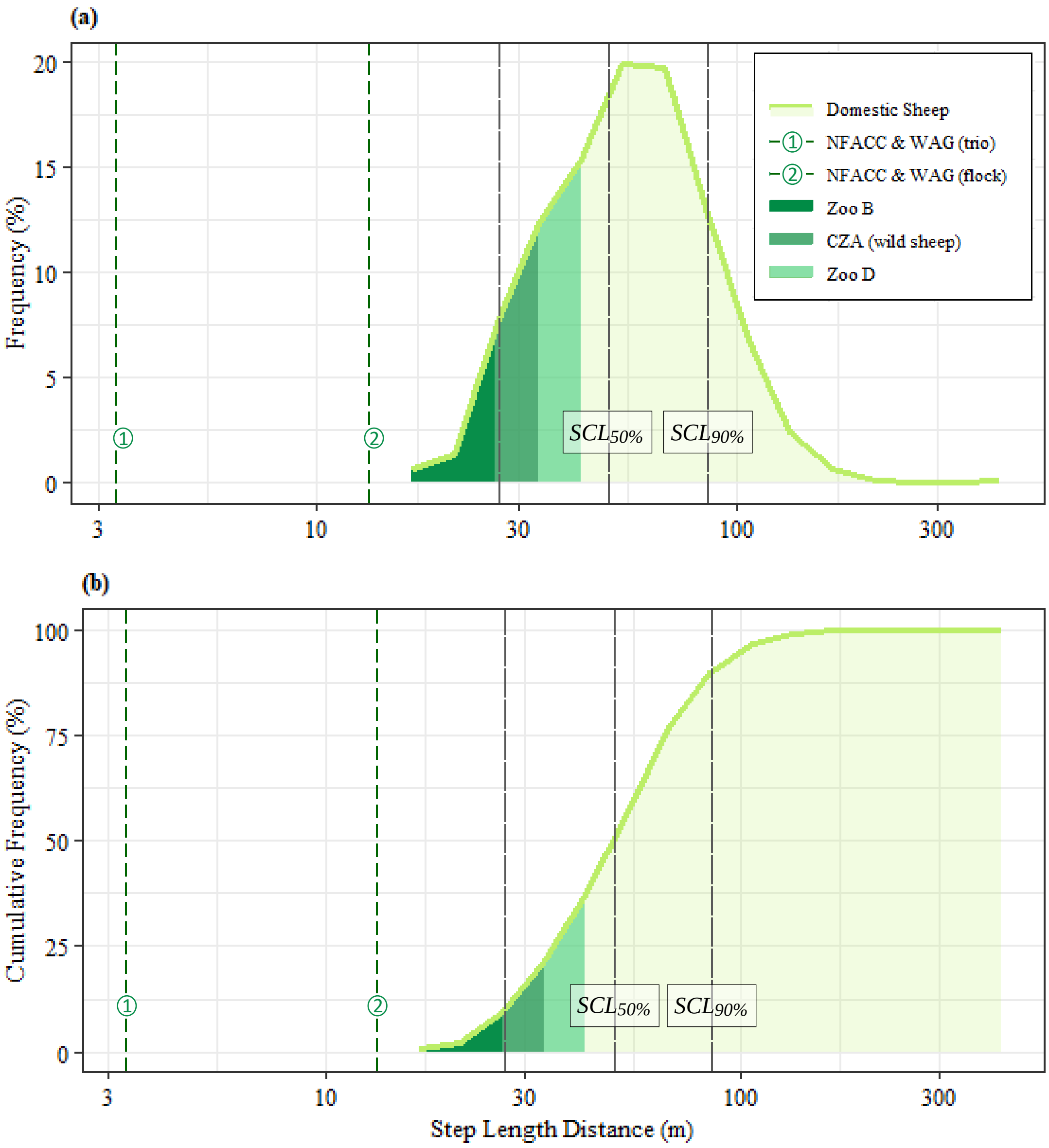

Figure 6. Step length distance data from three domestic sheep showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths (m). The vertical grey lines indicate where cumulative frequencies of 10 %, 50 % ($CSL_{50\%}$) and 90 % ($CSL_{90\%}$) fall in the data and correspond to step lengths of 27 m, 49 m and 85 m, respectively; step length distances ranging between 53–66 m were most frequent. Livestock guidelines (Table 4) set by the NFACC (2013) and WAG (2010) for a trio and a flock of 50 animals (3.3 m and 13.2 m corresponding to green dotted lines, 1 and 2, respectively) were below all recorded step length distances. In contrast, guidelines set by CZA (2014) for wild sheep giving 35.3 m allowed up to 24.8 % of step lengths, whilst zoos' B and D, with corresponding enclosures of 25.9 m and 40 m, permitted 8.3 % and 33.2 % of step lengths, respectively. N.B. Step length distance (m) is presented on the log scale, hence the proportion of step lengths permitted within enclosures will appear greater than it is.

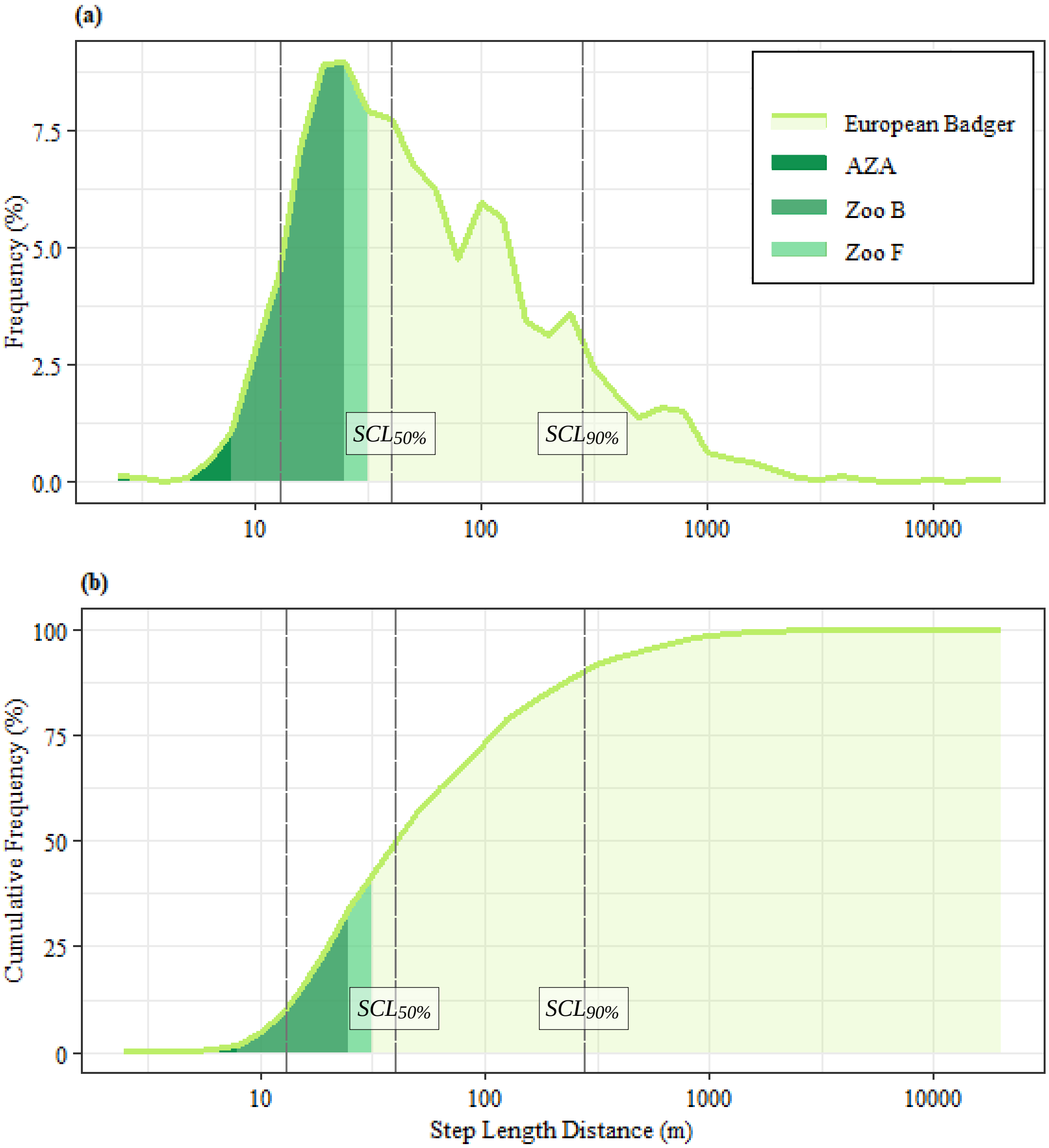

Figure 7. Step length distance data from five European badgers showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths (m). The vertical grey dashed lines indicate where cumulative frequencies of 10 %, 50 % ($CSL_{50\%}$) and 90 % ($CSL_{90\%}$) fall in the data and correspond to step lengths of 13 m, 40 m and 277 m, respectively. The highest frequencies of step length occurred at about 20–25 m and the maximum was approximately 19,860 m. Note that AZA Small Carnivore TAG (2010) guidelines (8.6 m; darkest green) accounted for 2.8 % of recorded step lengths undertaken by badgers whereas Zoo B, with an enclosure length of 27.1 m and Zoo F with one of 34.1m accounted for approximately 36.5 % and 44.3 %, respectively. N.B. Step length distance (m) is presented on the log scale, hence the proportion of step lengths permitted within enclosures will appear greater than it is.

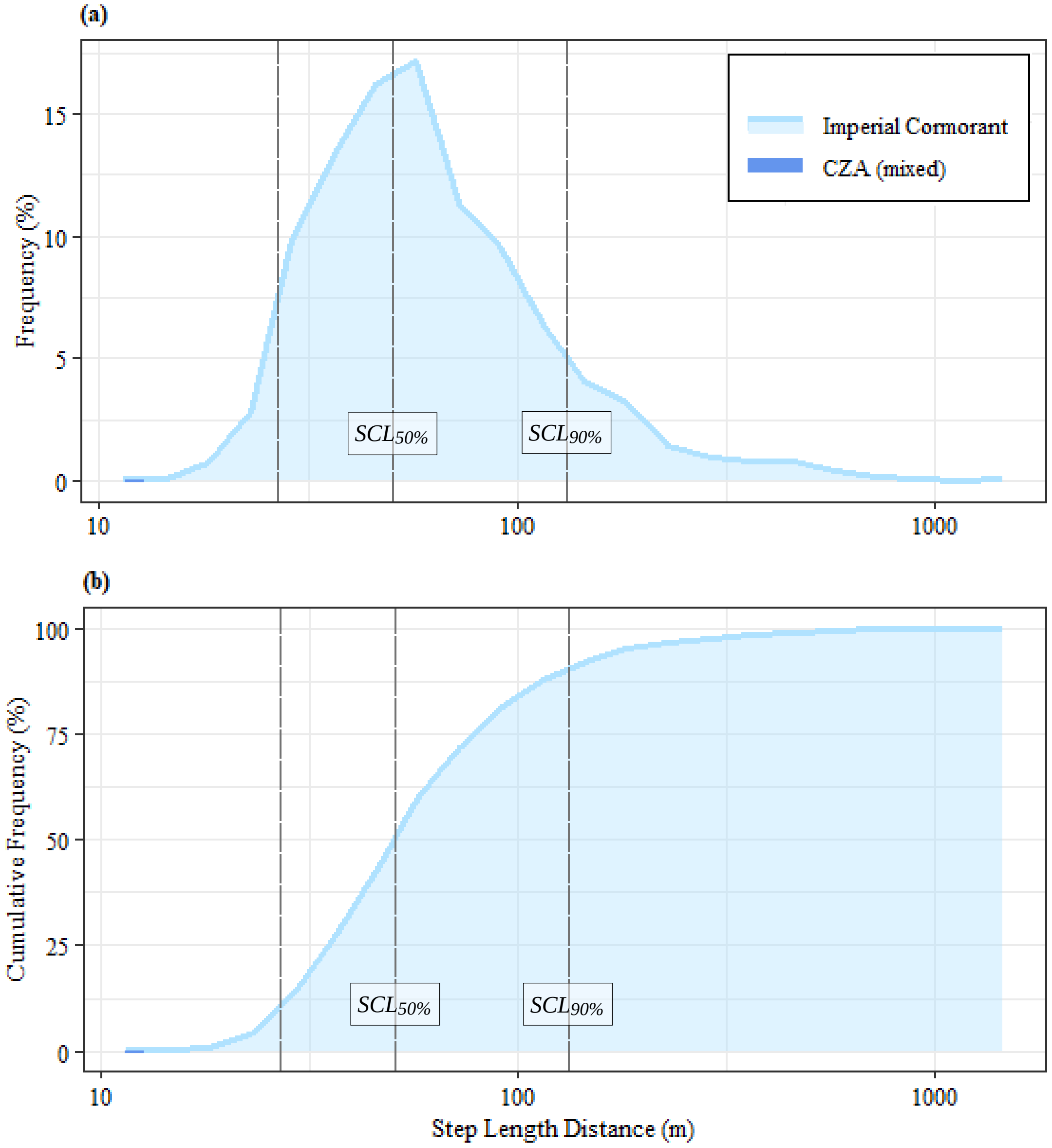

Figure 8. Step length distance data from five imperial cormorants whilst swimming, showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths (m). The vertical grey dashed lines indicate where cumulative frequencies of 10 %, 50 % ($CSL_{50\%}$) and 90 % ($CSL_{90\%}$) fall in the data and correspond to step lengths of 27 m, 50 m and 131 m, respectively. The highest frequencies of step length occurred at about 46–58 m. Pool size guidelines set by CZA (2014) for a mixed species, water bird exhibit (12.3 m long) only allowed up to 0.1 % of step length distances. N.B. Step length distance (m) is presented on the log scale, hence the proportion of step lengths permitted within enclosures will appear greater than it is.

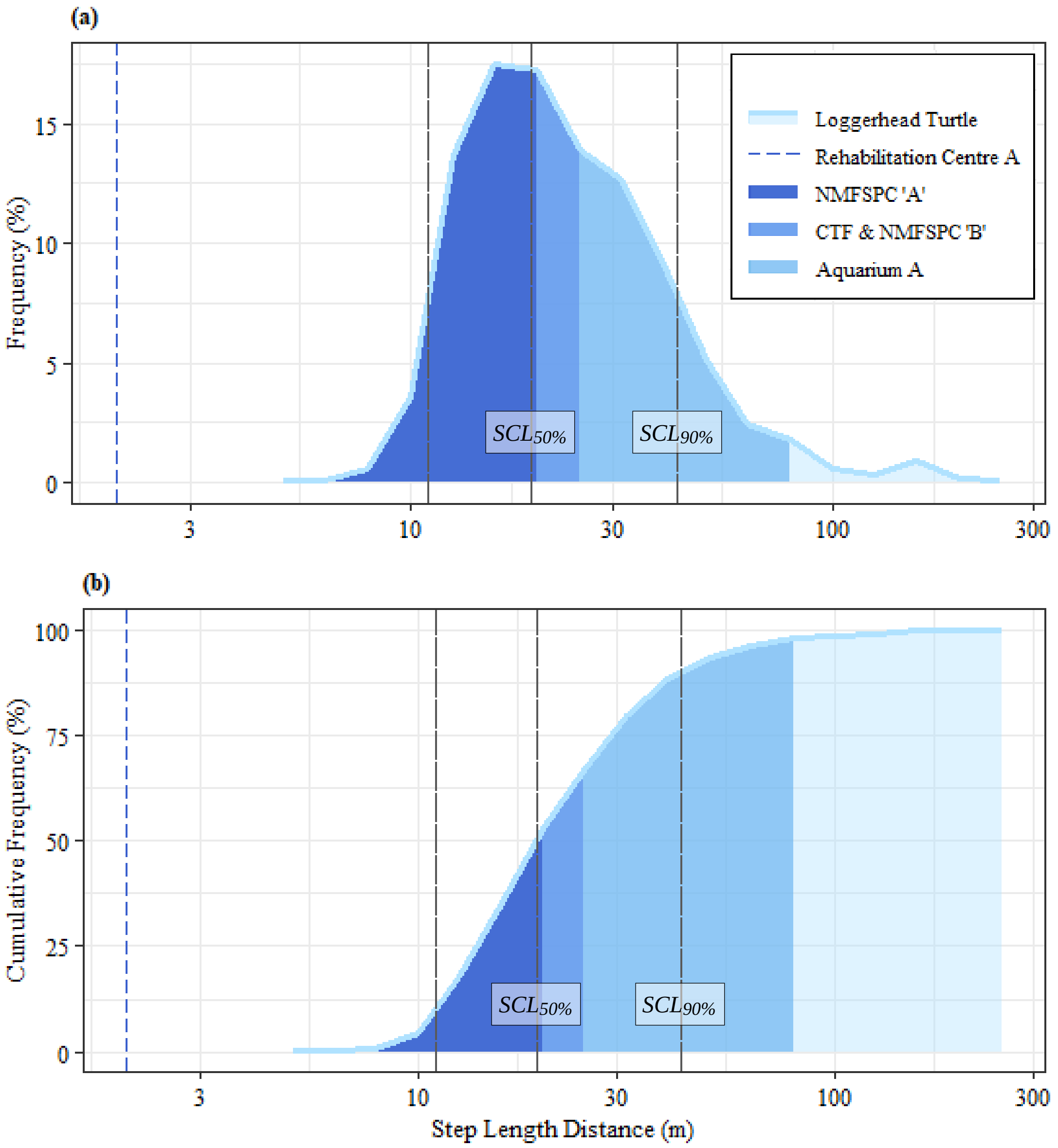

Figure 9. Step length distance data from five loggerhead turtles showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths (m). The vertical grey dashed lines indicate where cumulative frequencies of 10 %, 50 % (CSL$_{50\%}$) and 90 % (CSL$_{90\%}$) fall in the data and correspond to step lengths of 11 m, 19 m and 43 m, respectively. The highest frequencies of step length occurred at about 15–20 m. Small rehabilitation centre tanks (2 m diameter; dotted blue line) were smaller than the shortest recorded step length distances. Tanks for head-starting turtles at the National Marine Fisheries Service Panama City (NMFSPC) facility and the Cayman Turtle Farm (CTF), ranged between 19–24 m (Higgins 2002) and allowed 48.5–62.8 % of step lengths, whereas aquarium A (which had an 82 m long mixed species tank) permitted 98 %.

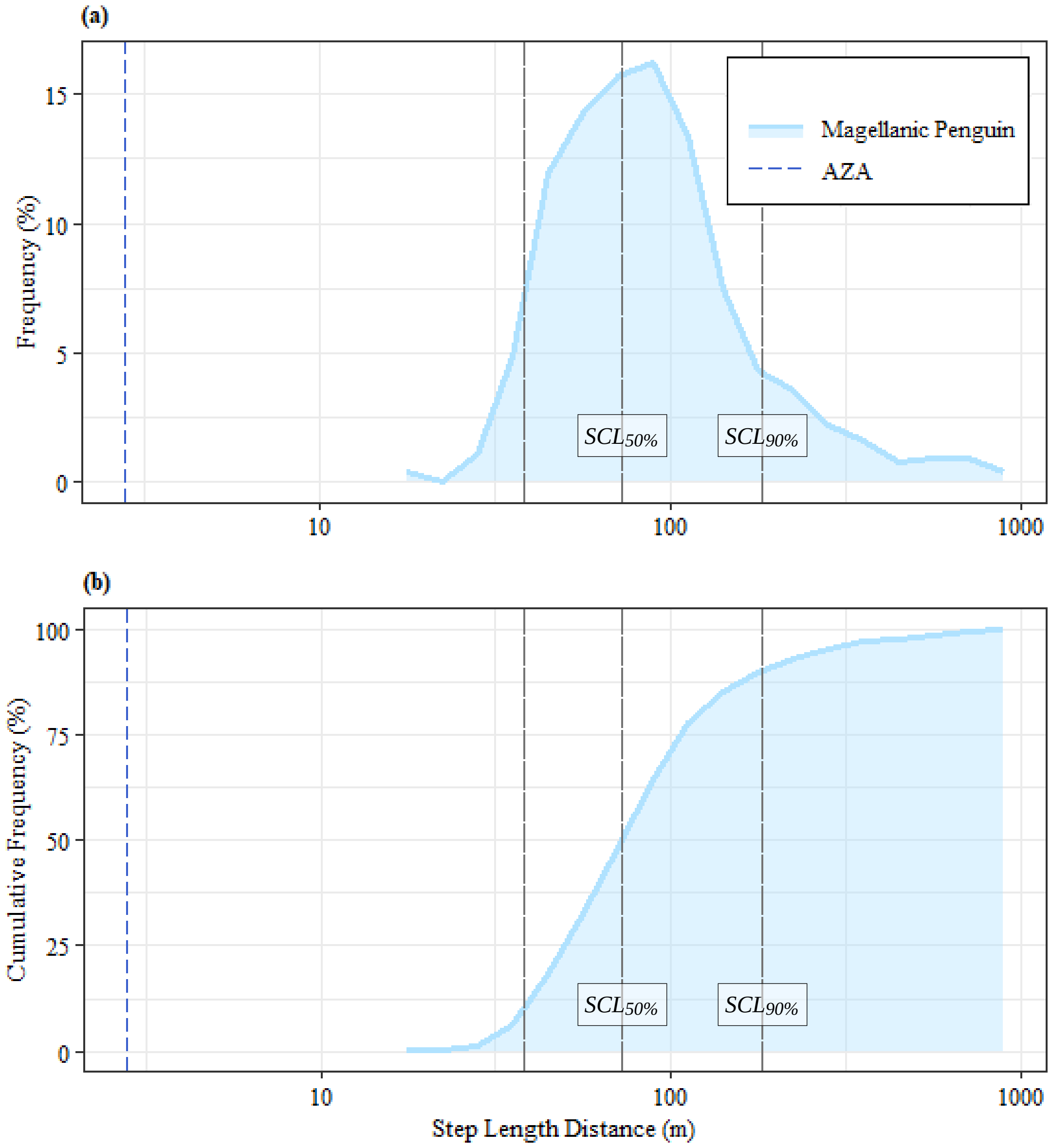

Figure 10. Step length distance data from five Magellanic penguins showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths (m) whilst swimming. The vertical grey dashed lines indicate where cumulative frequencies of 10 %, 50 % ($CSL_{50\%}$) and 90 % ($CSL_{90\%}$) fall in the data and correspond to step lengths of 38 m, 73 m and 182 m, respectively. The highest frequencies of step length occurred at about 53–67 m. Pool size guidelines set by AZA Penguin TAG (2014) for a minimum of 10 birds (2.8 m; blue dotted line) were below all recorded step length distances (meaning that they would fail to permit even 0.4 % of distances travelled). N.B. Step length distance (m) is presented on the log scale, hence the proportion of step lengths permitted within enclosures will appear greater than it is.

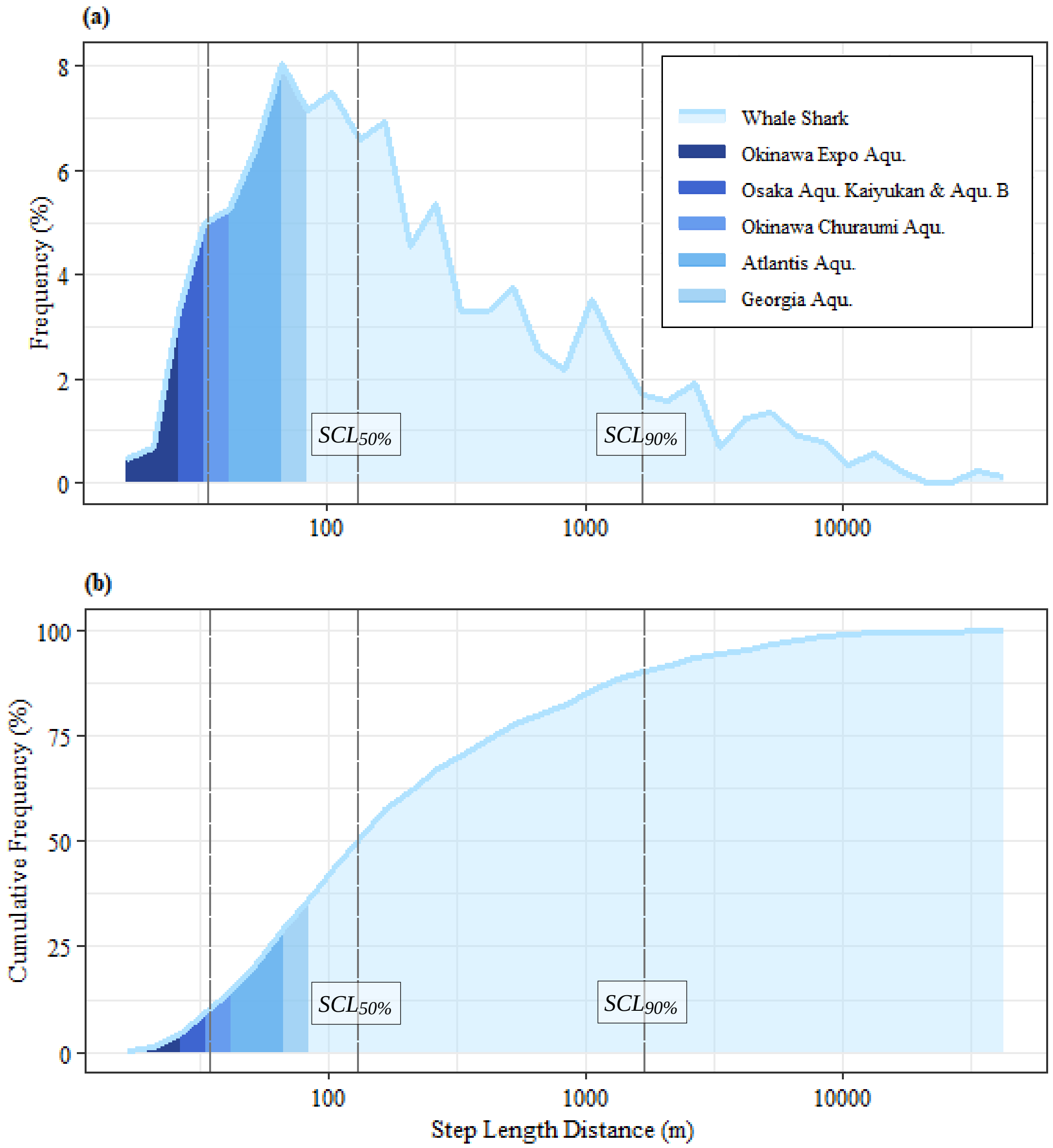

Figure 11. Step length distance data from five whale sharks showing the (a) frequency (%) and (b) cumulative frequency (%) of step lengths (m). The vertical grey dashed lines indicate where cumulative frequencies of 10 %, 50 % (CSL$_{50\%}$) and 90 % (CSL$_{90\%}$) fall in the data and correspond to step lengths of 34 m, 131 m and 1,676 m, respectively; the highest frequencies observed occurred around the 66–80 m mark. Aquarium B (aquarium abbreviated to 'Aqu.') with a tank 35 m could accommodate 10.4 % of step lengths. The largest tank, 84.2 m long at Georgia Aquarium could accommodate 36.4 % of recorded step lengths. N.B. Step length distance (m) is presented on the log scale, hence the proportion of step lengths permitted within enclosures will appear greater than it is.

4. Discussion

4.1 Step length and enclosure size

The purpose of this study was to investigate what proportion of step lengths in free-living animal movement could be undertaken in existing enclosure sizes and guidelines. As part of this, a primary goal was to create an index, termed '*ReMI*', utilising step length data from free-living animals compared to enclosure sizes, so that zoos could understand the restriction imposed on 'normal animal movement' by their enclosures. Based on previous findings that animals with wide-ranging behaviour are least suited to captivity and are most likely to display stereotypic or abnormal behaviours (Clubb & Mason 2007; Breton & Barrot 2014), another objective was to present information on species that may normally require so much space that they are unlikely to be suited to captivity.

This could well be the case for Andean condors, which displayed by far the longest step length distances: even the largest recorded Andean condor enclosure in North America at 30.5 m long (2007–2008 AZA Andean Condor SSP exhibit survey; AZA Raptor TAG (2010)) only permitted less than 0.2 % of recorded step lengths ($ReMI_{CSL\_90} < 0.01$; Figure 3). The same exhibit survey found that the average enclosure lengths totalled 16.5 m and based on this the AZA Raptor TAG Andean condor care manual (2010), suggested that this should be the minimum size. Considering that only 10 % of Andean condor step lengths were below 504 m (the rest were above) and that they had a $CSL_{50\%}$ of 1,834 m (which if implementing a $ReMI_{CSL\_50\%} \geq 1$ would be the absolute minimum 'adequate' enclosure size), let alone a $CSL_{90\%}$ of 12,647 m (!), such relatively small enclosures are likely to have adverse effects on behaviour and well-being.

Whale sharks displayed the second longest step length distances with a $CSL_{50\%}$ and a $CSL_{90\%}$ of 131 m and 1,676 m, respectively. These *CSL* measurements strongly indicate that whale sharks in captivity may require substantially less space than Andean condors (*cf.* Figures 3 and 11). However, given that whale sharks are much larger in size, it is not surprising that they are generally afforded more space in captivity. Existing tanks sizes at six different aquariums (ranging from 29.5–84.2 m), permitted 6.6–36.4 % of step length distances to be realised. The average of these tank sizes, 50.5 m, would have permitted approximately 20% and of step lengths yielding a $ReMI_{CSL\_50\%} = 0.39$ and a $ReMI_{CSL\_90\%} = 0.03$ (both of which would be considered undersized according to the thresholds of $ReMI_{CSL\_50\%} \geq 1$ and $ReMI_{CSL\_90\%} \geq 0.5$ set for this study).

Five of the six tank sizes were taken from the Elasmobranch Husbandry Manual (Smith et al. 2004; 2017) which, despite providing detailed information on a range of husbandry issues (e.g., nutrition and feeding, transport and handling, medical procedures and treatment, reproductive technologies as well as tank construction, design and enrichment), for a variety of elasmobranch species, gave no enclosure size recommendations based on up-to-date scientific investigations. The Elasmobranch Husbandry Manual (Smith et al. 2004; 2017) does cite a formula for minimum tank dimensions developed by Klay (1977) for common collector sharks (species including bull sharks, *Carcharhinus leucas*; lemon sharks, *Negaprion brevirostris*; nurse sharks, and sandbar sharks, *Carcharhinus plumbeus*) however its basis is 'relatively unscientific' (Choromanski 2004). This is one of multiple examples where an index which does have a scientific basis, such as *ReMI*, could be implemented as part of an integrative managed care approach.

Just as with whale sharks, scientifically grounded enclosure size recommendations were also lacking for loggerhead turtles, although Higgins (2002) does detail and advise following the stocking densities and pen dimensions implemented at a couple of head-starting facilities (*cf.* Table 4). These ranged between 18.9–23.6 m ($ReMI_{CSL\_90\%} = 0.44–0.55$, values just below and above the 'adequate' threshold) and allowed 48.5–62.8 % of natural step lengths to be realised. Turtles housed in an 82 m long, mixed species exhibit ($ReMI_{CSL\_90\%} = 1.9$; Figure 9, aquarium A) were able to realise 98 % of their natural step lengths (well above the 'suitable' threshold: $ReMI_{CSL\_90\%} \geq 0.9$). Loggerhead turtles were found to have the shortest $CSL_{50\%}$ and $CSL_{90\%}$ of all study animals, (19 m and 43 m, respectively), making them potentially good candidates for captivity. The Arabian oryx also displayed relatively short step lengths ($CSL_{50\%}$ and $CSL_{90\%}$ of 30 m and 65 m, respectively) and were able to conduct 98.8 % of their step lengths within a large mixed species enclosure which was 143 m long ($ReMI_{CSL\_90\%} = 2.2$; Figure 5). But despite having comparably short step lengths minimum AZA Antelope TAG (2001) requirements were only sufficient for 1–2.3 % of step lengths to be realised, indicating that current guidelines may even be too small for animals with short step lengths.

Space recommendations for domestic sheep and European badgers, animals with medium range step lengths ($CSL_{50\%}$ of 49 m and 40 m, and $CSL_{90\%}$ of 85 m and 277 m, respectively), were also restrictive. Even pen guidelines for a flock of 50 sheep at 13.2 m long (WAG 2010; NFACC 2013) permitted less than 0.7 % of step lengths and exhibit guidelines for European badgers with a longest length of 8.6 m (AZA Small Carnivore TAG 2010) allowed 2.8 %. As observed for all study animals, even the smallest zoo enclosure sizes (for example, 25.9 m long for domestic sheep and 27.1 m long for European badgers) were larger than recommended size guidelines, nonetheless, both were often undersized according to the minimum threshold ($ReMI_{CSL\_50\%} = 1$) set in this study.

The Aldabra giant tortoise (another animal that covered relatively short straight-line distances, with a $CSL_{90\%}$ of 51 m) was the only study species for which existing guidelines accommodated more than 3 % of step lengths: CZA (2014) exhibit recommendations, with an estimated longest length of 22.4 m, permitted up to 61.9 % of step lengths and hovered around the ‘acceptable’ size threshold with a $ReMI_{CSL\_50\%} = 1.2$ and a $ReMI_{CSL\_90\%} = 0.4$ (the latter being just below the 0.5 threshold). Implementing both *ReMI* versions would give zoos some extra flexibility whilst also indicating whether the $CSL_{50\%}$ can be realised (or is at least close to being realised) when the $CSL_{90\%}$ cannot (see section 4.2 for a discussion on different ways *ReMI* could be adjusted).

4.2 Shifts in behavioural mode and adjusting *ReMI* for purpose

A plausible next step for enhancing captive environments further may be to improve and apply our understanding of free-living animal movement patterns (Clubb & Mason 2007; Breton & Barrot 2014) and the behavioural plasticity present among wild conspecifics (Melfi & Feistner 2002; Mehrkam & Dorey 2015; Chatpongcharoen et al. 2021). Collecting step length distribution allows us to study how animals behave, potentially giving valuable insights into their basic movement instincts, needs and trajectories. Central to this is that animals change direction according to environmental stimuli (Potts et al. 2018) so various distributions may reflect the distribution of elicitors. Moreover, peaks and troughs in frequency distributions show which distances are most commonly travelled and may represent important shifts in behavioural modes– e.g., commuting *versus* foraging peaks.

The majority of study animals had relatively uncomplicated step length distributions with one clear peak in the data (*cf.* Aldabra giant tortoise, Arabian oryx, domestic sheep, imperial cormorants and Magellanic penguins; Figures 4, 5, 6, 8 and 10, respectively). If prominent peaks do represent important step length distances, defining adequate enclosure sizes that can accommodate important movement behaviours should, in theory, be relatively straight forward. In this case, marked declines in step length frequency may indicate key thresholds for enclosure size and *ReMI* could be tailored accordingly. For instance, marked declines which occur beyond 28 m for Aldabra giant tortoise and beyond 52 m for Arabian oryx (with each remaining data bin always accounting for less than 10 % of step lengths), may indicate viable enclosure sizes and would translate to a $ReMI_{CSL\_90\%}$ = 0.55 and a $ReMI_{CSL\_90\%}$ = 0.8 respectively.

Applying this principle to animals with multiple peaks and troughs in their step length frequency distributions (*cf.* Andean condors, European badgers and whale sharks; Figures 3, 7, 11) is more complex. However, if peaks are biologically meaningful (the probability of this could be tested statistically), a simple count of the number of peaks that occur within and fall outside of a given enclosure size could be done to give some measure of enclosure adequacy. Peaks that are small and hard to distinguish might have to be dealt with on a case-by-case basis, but potential workarounds might involve only using obvious peaks when informing enclosure size or looking at where the decline trend in the frequency distribution changes angle (i.e., becomes less steep).

A working example of how peaks could be used to inform enclosure size is as follows: to accommodate the three main peaks in the Andean condor step length frequency distribution (Figure 3), an enclosure would have to be 4,560 m long: this would equate to a $ReMI_{CSL\_90\%}$ = 2.49 (much higher than the threshold of 0.5 used in this study). Whereas an enclosure big enough to accommodate the two major peaks in the European badger step length data (Figure 7) would have to be 63 m long: this would correspond to a much lower threshold ($ReMI_{CSL\_90\%}$ = 0.28). Accommodating the first five main peaks in the whale shark step length data (Figure 11; which would require a 266 m long enclosure) also translates to a much lower threshold ($ReMI_{CSL\_90\%}$ =

0.16). However, before implementing this kind of strategy within a zoo context, scientists working in the field would need to work out whether peaks did represent different modes of behaviour and what those modes were. Next it would need to be established if they were likely to be important to an animal's well-being or not.

Another way in which *ReMI* could be adjusted for different species is by setting different limits of *CSL* as was trialled in this study ($ReMI_{CSL\_90\%} \geq 0.5$ and $ReMI_{CSL\_50\%} \geq 1$ represented enclosures of an 'adequate' size). It is important to note, however, that implementing '$ReMI_{CSL\_50\%} \geq 1$' would be more favourable for animals with step length distributions that attain high cumulative frequencies quickly and peak before the $CSL_{50\%}$, as opposed to animals with longer step length distances, more evenly dispersed frequency distributions and higher frequencies above the $CSL_{50\%}$. For example, domestic sheep with a $CSL_{50\%}$ and a $CSL_{90\%}$ of 49 m and 85 m would be less constricted by the implementation of $ReMI_{CSL\_50\%} \geq 1$ (which would equate to a 49 m long enclosure), than European badgers with a $CSL_{50\%}$ and a $CSL_{90\%}$ of 40 m and 277 m.

Whilst implementing different *ReMI* thresholds would give zoos some extra flexibility, it would be important to assess suitable levels of movement restriction for different species. Especially because just a few metres can make a big difference to the percentage of step lengths permitted, for instance, domestic sheep in a 25.9 m long enclosure would only be able to realise 8.3 % of their step lengths whereas in a 40 m long enclosure they would be able to realise 33.2 %. Given that restricting animal movement has a wide variety of potential adverse effects there are multiple aspects of behaviour (e.g. stereotypic behaviours like pacing or head rolling (Mason & Rushen 2008; Breton & Barrot 2014), distance travelled (Hampson et al. 2010b), activity level (Galef Jr et al. 2006; Mallapur et al. 2009) and breeding success (Clubb & Mason 2007; Marshall et al. 2016) but see section 4.3) that could be used to inform enclosure size and set best practice standards for captivity.

4.3 How might constricting step lengths affect animals?

Although zoo enclosures are designed with species-specific behaviour, physiology and space requirements in mind (Ross et al. 2009; Phillips et al. 2011; Campbell-Palmer & Rosell 2015; French et al. 2018) animals in captivity will undoubtedly have less space in which to move than wild conspecifics (average enclosure size in the UK was found to be 100 times smaller than the minimum home range (Casamitjana 2003)). Comparisons between animals with short step lengths and those that are far ranging demonstrate how the former are afforded relatively more much space in captivity than the latter; reported enclosure sizes for loggerhead turtles, Arabian oryx and Aldabra giant tortoise allowing 25–98.8 % of step length distances juxtapose even the vary largest Andean condor enclosure allowing 0.9 % step lengths. In order to understand the effects of constricting animal movement it may also be important to understand why free-living animals have step lengths of varying magnitude. Typically, distance travelled reflects resource distribution with animals in arid conditions travelling for days in order to reach sources of water (Hampson et al. 2010a) and carnivores roaming several kilometres in order to hunt sufficient prey (Karanth & Nichols 2010). Many species also undertake physiologically challenging migrations, sometimes hundreds of kilometres long, to reach new foraging and/or mating grounds (Petersons 2004; Linnane et al. 2005; Fossette et al. 2008; Boyle et al. 2009; Bowlin et al. 2010; Guo-Gang et al. 2011; Abrahms et al. 2019)

The potential effects of restricting movement are not well understood or documented but can at the very least lead to animals being more sedentary which over the long-term may have implications for metabolism, physiology and overall well-being (Hampson et al. 2010a). Animals kept in small enclosures have been shown to be less active: on average horses (*Equus caballus*), kept in small yards travelled only 1.1 km/day whilst others in a 16-hectare paddock travelled 7.2 km/day (Hampson et al. 2010b). In contrast feral horses travelled 15.9 ± 1.9 km/day (Hampson et al. 2010a). Animal confinement in combination with altered feeding (Richards et al. 2006) mirror the modern human lifestyle, which is believed to be behind endemic levels of obesity, cardiovascular disease, arthritis, and diabetes (*cf.* Power 2012; Mainous et al. 2019), and these diseases are ever-increasingly observed in captive animals (Johnson et al. 2004; Perkins et al.

2005; Goodchild & Schwitzer 2008; Harris et al. 2008; Lepeule et al. 2009; Lepeule et al. 2013; Feldmann 2016).

Restricting animal movement has been linked to various issues in captivity, especially in animals with large home range sizes (Clubb & Mason 2007). A study of 38 captive tigers (*Panthera tigris*) found that abnormal behaviours, such as pacing, increased with decreasing enclosure size and could develop as soon as animals were old enough to disperse (Breton & Barrot 2014). The same study created a tiger movement index (subtracting the distance paced from the total distance covered and then dividing by the total distance covered) for zoos to use as a tool to quantify and reduce abnormal pacing– the premise of the movement index being similar to *ReMI* in that it was designed to guide enclosure size.

Wide-ranging behaviour is also a predictor for relatively high captive infant mortality rates in carnivores; to combat this, exhibits are advised to offer numerous den sites, high environmental changeability, and additional space (Clubb & Mason 2007). In fact, multiple studies report increased enclosure size having a positive effect on captive animal behaviour, especially with regard to activity level (Perkins 1992; Veasey et al. 1996b; Mallapur et al. 2005; Galef et al. 2006; Mallapur et al. 2009; Marshall et al. 2016) and species-typical behavior (Melfi & Feistner 2002; Ross et al. 2009; Brummer et al. 2010; Marshall et al. 2016; Howell & Cheyne 2019). For example, Humboldt penguins, *Spheniscus humboldti*, in bigger exhibits not only swim more (which promotes physical health) but also have better prospects for colony growth as breeding success increases with mate choice and the number of breeding pairs an enclosure can house (Marshall et al. 2016).

In fact, breeding success in captivity has been routinely used as a measure of animal welfare (primates: Abello and Colell, 2006; carnivores: Clubb and Mason, 2007; birds: Farrell et al., 2000; invertebrates: Wisniewski, 2000). Conversely, poor breeding success is commonly linked to sub-optimal conditions, confinement induced stress (Peng et al. 2007; Descovich et al. 2012) and a lack of opportunities for social interaction (Mallapur et al. 2006; Nicholas, 2007; Swaisgood & Schulte 2010). Nonetheless, breeding success alone does not ensure animal welfare (Swaisgood 2007) hence the ever-increasing use of behavioural indicators for physiological and psychological well-being, (for example, whether an animal is fearful, dominant, cooperative, affectionate or calm (Hancocks 2010; Kelling & Gaalema 2011; Gartner 2014; Gartner et al. 2016; Quintavalle Pastorino et al. 2017) as well as the continued use of activity budgets in welfare assessments (Melfi & Feistner 2002; Wark et al. 2019).

Captive animals welfare may also be assessed through markers of stress such as elevated heart rate (Ropert-Coudert et al. 2009; Brummer et al. 2010; Fischer et al. 2016) and glucocorticoid secretion (Li et al. 2007; Schwarzenberger 2007; Mason & Veasey 2010; Piñeiro et al. 2012; Vick et al. 2012) which are often exacerbated by increased proximity to humans. Bigger enclosures with appropriate enrichment, allowing animals to retract and hide, can alleviate these stress related responses but may also detract from visitor experience if animals cannot be seen (although generally speaking animals do not stay hidden all of the time (*cf.* Shelbourne 2010; Fischer et al. 2016)). Another issue closely linked to stress is that of disease; captive cheetahs (*Acinonyx jubatus*) are prone to unusual infectious and inflammatory diseases (rarely observed in free-living animals) that cause morbidity and death and are thought to be linked to chronic stress (Terio et al. 2004). Similarly, the high levels of morbidity and mortality observed in captive orcas (*Orcinus orca*), are also thought to stem from chronic stress and its effect on physiology and illness (Marino et al. 2020). Bottlenose dolphins (*Tursiops truncatus*), too, suffer stress induced health consequences with implications for blood profiles, loss of appetite, gastric ulcers, social stability, and mortality (Waples & Gales 2002). Captivity is likely to be particularly stressful for these wide-ranging animals (Casamitjana 2003; Clubb & Mason 2007) whose movement needs extend far beyond a few metres.

Zoo enclosures are undoubtedly bigger than they once were with a lot more thought given to whether animals should be housed solitarily or not (*cf.* Benbow 2000, 2004; Ross et al. 2009; AZA Raptor TAG 2010; AZA Lion Species Survival Plan 2012; AZA Penguin TAG 2014; AZA Charadriiformes TAG 2014; 2018). After decades of negative publicity and pressure from activist groups and the public alike, wide-ranging mammal species like polar bears (*Ursus maritimus*) and elephants (*Loxodonta africana*) are no longer confined to small inadequate enclosures as they once were (*cf.* Hancocks 1980; Jensvold et al. 2001; Tribe & Booth 2003; Swaisgood & Shepherdson 2005; Finch et al. 2020)– take the three polar bears and the lone elephant that were once maintained at Bristol Zoo– a small, 12-acre, urban zoo (Flack 2016). But, despite obvious improvements to animal husbandry in recent decades, the number of zoos that meet all up-to-date requirements may be low and vary greatly with location: a study conducted by Draper and Harris (2012) found that of 192 zoos in Britain, only 24% met all legislated welfare standards. Furthermore, the standards set may not fulfil animal needs– UK zoo elephants, which receive some of the highest standards of captive care, were found to be overweight/ very overweight (75 %), had multiple foot problems (42 %), were lame (23 %), and performed stereotypic behaviour during the day (26%) as well as at night (37%) (Harris et al. 2008). Issues with elephant obesity extend across Europe (Schiffmann et al. 2018) and North America (Morfeld et al. 2016).

Current standards for the three bird species in this study (Andean condors, imperial cormorants and Magellanic penguins) are also likely to fall short of their needs given that recommended space allowances did not permit even their smallest recorded step length distances. These findings are not unique as multiple studies have recommended substantial increases to enclosure size guidelines for a variety of species including elephants (Harris et al. 2008), tigers (Breton & Barrot 2014), coyotes (*Canis latrans*; Brummer et al. 2010), horses (Flauger & Krueger 2013), goats (*Capra aegagrus hircus*; Bøe et al. 2012), penguins (Marshall et al. 2016) and chickens (*Gallus domesticus*; Mallapur et al. 2009). Arguably, there is always more that can be done, and with complete control over captive animal management in terms of environmental surroundings and providing care, humans have a duty to ensure the welfare of captive animals (Minteer & Collins 2013; Benn et al. 2019).

4.4 Limitations of *ReMI*

Currently, a weakness of *ReMI* based on predefined *SCL* thresholds is that these thresholds may not be meaningful. For example, if pacing (*cf.* Clubb & Mason 2007; Breton & Barrot 2014) or another type of stereotypic behaviour (such as head rolling (Shyne 2006)) decreased in enclosures that could accommodate ≥ 70 % of step lengths it may make sense to apply a threshold of $ReMI_{CSL\_70\%} = 1$. It may also be of value to ascertain if the peaks in step length frequency graphs are representative of specific modes and behaviours (as mentioned in section 4.2). If peaks are biologically meaningful, assessing the proportion of peaks that lie within current enclosure guidelines and those that fall outside could also be useful. Another potential limitation of *ReMI* is that it focuses on straight-line distances travelled and does not consider angle extent at different turn points which could also have important implications for movement. With some research, however, suitable step length thresholds as well as turn extents could be defined for a number of species and then extrapolated to animals of similar sizes with similar movements patterns for which movement data is yet to be collected.

For the most part minimum size guidelines are likely to be smaller than current zoo enclosures (*cf.* Aldabra giant tortoise, Arabian Oryx and European Badger; Figures 4, 5 and 7) but beyond this, not much can be garnered given that sample sizes were small and there were no zoo enclosure sizes for a third of study animals (Andean condors, imperial cormorants, and Magellanic penguins). Sadly, of the 132 zoos and aquariums contacted, only 14 were willing to participate and sent enclosure size data. If this study had received support from either AZA, BIAZA or EAZA, at least another five zoos would have taken part (one of the many roles of zoological associations is to advise zoos on high priority research topics). Still, general uptake was obviously low which could be indicative of a lack of trust and cooperation between researchers and zoological institutions.

Despite enclosure sizes from all participating zoos being anonymised and the purpose of this work being to present data to help make animal exhibits more suitable, many of the zoos contacted were wary of partaking in this research, fearing that comparisons between free-living animal movement and enclosure sizes might reflect unfavourably on the latter. By the same token, BIAZA, the only association to respond to our application of support and following emails, declined to share any of their animal husbandry manuals, stating that guidelines typically refer to the ‘minimum required size’ rather than what is ‘expected’ and that enclosure size is ‘not necessarily a welfare indicator without considering a number of other factors about the enclosure and its inhabitants’. These statements are valid and whilst they do not negate the importance of exhibit size, they are understandable given that zoos and aquariums have limited space and are regularly scrutinized (Keulartz 2015). Building good relationships between zoological institutions and researchers may be fundamental when conducting investigations that require data sharing (Hutchins & Smith 2003; Fernandez & Timberlake 2008; Kubarek & Johnson 2022).

Aside from obtaining few enclosure sizes for comparison, the number of animals from which step length data was collected was also small (between 3–7 individuals per species). Still, this study introduces a novel concept rather than a finished product and I feel it is a good starting point. It is not unusual for studies with large vertebrate species to have small sample sizes ranging between 5–20 animals (Ropert-Coudert & Wilson 2005; Wilson et al. 2005; Brown et al. 2013; Wilson et al. 2018; Gunner et al. 2020; Williams et al. 2020; Wilson et al. 2021a; Gómez-Laich et al. 2022) and this is for a variety of reasons; first, according to the 3 Rs (replacement, reduction and refinement), as few animals as possible should be tagged (Russell & Burch 1959), second, tagging equipment is expensive and third, access to both wild and captive animals is often limited, particularly in captivity where few individuals are kept (Swaisgood & Shepherdson 2005; Kuhar 2006). Still, cooperation between researchers and zoological institutions and data sharing would help augment group sizes for biologically meaningful results.

4.5 How might captive environments be enhanced?

Zoo enclosures are designed to provide for the animal's physical, social, and psychological well-being (AZA Accreditation Standard 10.3.3) and to take into account natural behavioural repertoires, space requirements and social needs (Burghardt et al. 1996; Case et al. 2005; EAZA Standards for the Accommodation and Care of Animals in Zoos and Aquaria 2014; 2020; Mellor & Beausoleil 2015; Bashaw et al. 2016; Alba et al. 2017). Animal care manuals give detailed information pertaining to animal nutrition, blood values, transportation and social requirements as well as suitable enclosure design and enrichment, including which materials are safe to use and desirable exhibit structures like shelters, pools and vegetation (AZA Antelope TAG 2001; AZA Chiropteran TAG 2004; Smith et al. 2004; 2017; AZA Small Carnivore TAG 2009; AZA Lion Species Survival Plan 2012; AZA Penguin TAG 2014; Mellor et al. 2015; AZA Charadriiformes TAG 2018). All these fields are discussed at length, often without defining space requirements or giving movement needs much thought (see: Gilbert & Woodfine 2004; AZA Wild Pig, Peccary and Hippo TAG 2008; AZA Pelecaniformes TAG 2012; Smith et al. 2004; 2017; EAZA 2014; 2020; Náhlik et al. 2017; De Kock et al. 2018; EAZA Tapir and Suiform TAG 2018; Varga 2019; AZA Rodent, Insectivore and Lagomorph TAG 2021) and when guidelines are included they are sometimes based on existing enclosure sizes (Higgins 2002; AZA Raptor TAG 2010; AZA Charadriiformes TAG 2014) rather than a scientific framework that takes into account the movement requirements of a given species.

Unsurprisingly, current top priorities for zoos and aquariums align closely with the issues discussed in care manuals and centre on providing appropriate environmental stimuli, opportunities for behavioural expression and nutrition, which are key to animal well-being and mental state (Burghardt et al. 1996; Mellor & Beausoleil 2015; Bashaw et al. 2016). This being the case, it would also seem practical to consider how far and how fast an animal travels. For example, an Andean condor in a ~220 m long aviary (contrasting one that is only 16.5–30 m) cannot move remotely as it would in the wild. Can captive environments really provide it with sufficient opportunities for behavioural expression? The same question applies to whale sharks in 30–85 m tanks and water birds (like imperial cormorants and Magellanic penguins) with access to shallow pools that are only a few metres long.

Asking these types of question seems timely given the pressure on zoos to maintain high welfare standards, particularly with regards to mammals and other large vertebrates (Rose et al. 2017a; Rose et al. 2017b; Shorter et al. 2017). As discussed previously, constricting animal movements can be linked to a wide variety of adverse effects (section 4.3) which could be alleviated by quantifying free-living animal behaviour and using it to inform enclosure design. This approach compliments moves to consider species-specific needs and encourage more diverse behaviour (Burghardt et al. 1996; Case et al. 2005; Mellor & Beausoleil 2015; Bashaw et al. 2016; Alba et al. 2017; Bacon 2018; Chatpongcharoen et al. 2021).

Studies could begin looking at the consequences of stopping an animal before it can fulfil a certain percentage of its step lengths by asking questions like: ‘Does the incidence of stereotypic behaviour correlate with step length?’ and ‘Is pacing a function of step length distribution?’. Investigating these themes may reveal if a $CSL_{50\%}$ or a $CSL_{90\%}$ would be sufficient or not and if certain species require different thresholds within the step length frequency distribution. These findings would be of biological significance and would be more meaningful than relying on statistical significance which is generally placed at 95 % (Nakagawa & Cuthill 2007). This study used critical points in the step length frequency distribution at the 50 % and 90 % limit– adopting a more flexible approach seemed like a sensible way of drawing comparisons given that minimum space guidelines were always far below 95 % of step lengths: for six out of nine species considered, less than 3 % of step lengths were realisable within existing enclosure guidelines (for Aldabra giant tortoise and loggerhead turtles over 60% of step lengths were realisable and for whale sharks no guidance on space was provided).

4.5.1 The space dilemma and ongoing challenges

Space is a luxury, more limited and expensive than ever before, especially for zoos that are often built on prime real estate in dense cities (Wildt et al. 2019). In conjunction with growing concerns regarding animal welfare, zoos have moved towards creating elaborate exhibits with fewer animals which may be behind declines in cooperatively managed AZA zoo populations of mammals (45 %) and birds (35 %) as well as amphibians and reptiles (34 %) (Long et al. 2011). However, the task of providing safe space for an ever-increasing number of animals as wild populations dwindle is in direct conflict with reducing numbers in captivity to promote welfare (Monfort et al. 2018; Powell 2019). Unfortunately, zoos do not currently have the capacity necessary to be able to sustain rare species in secure populations, prevent extinctions and source reintroduction projects all while generating new knowledge (Conway 2011; Lacy 2013). For instance, in the whole of North America a modest 43.1 km^2 of zoo land exists (emanating from 158 AZA accredited urban institutions averaging less than 0.3 km^2 each) to meet the needs of thousands of wildlife species in terms of breeding, exhibition, education, merchandizing, and other zoo-related issues (Wildt et al. 2019).

It was noted over 40 years ago that city zoos were ‘land poor’ and that rural breeding farms and ranches would be needed to supplement zoo populations and maintain genetic diversity (Conway 1980). Indeed, this approach would ease some issues related to space and population viability (Wildt et al. 2019). However, ensuring animal welfare standards, including providing enough room for species under human care should remain a top priority, especially because stereotypic behaviours in carnivores, such as pacing, are significantly predicted by natural ranging behaviour (e.g., home-range size and typical daily travel distances) instead of foraging or hunting behaviour as is often believed (Clubb & Mason 2007).

Perhaps the best way to begin ensuring enclosures are adequate is by choosing animals with small ranges whose needs can be met in captivity and this may mean assessing from a movement perspective which animals are most appropriate (Clubb & Mason 2007). Although few publications explore this, some mammals that typically fare well in captivity as suggested by Taxon Advisory Group reports and ISIS database figures (http://www.isis.org) are: American mink (*Neovison vison*), snow leopards (*Panthera uncia*), brown bears (*Ursus arctos arctos*), ring-tail lemurs (*Lemur catta*, (Petter 1975)) and rhesus macaques (*Macaca mulatta* (Primack 1998)). Whilst studies may not investigate the suitability of a species to captivity outright, assessments of well-being in captivity, *via* behaviour profiles (including openness to experience, extroversion, agreeableness and neuroticism (Quintavalle Pastorino et al. 2017)) cognitive bias (Bethell et al. 2012) and personality traits (i.e., whether an animal is affectionate, calm, cooperative, dominant or fearful (Gartner 2014; Gartner et al. 2016)) are on the rise.

With increasing animal welfare and conservation awareness paired with a desire to see large mammals and endangered animals (Carr 2016), it is not surprising that the numbers of people visiting safari parks and nature parks is ever increasing (Butt 2012; Ferreira & Harmse 2014; Prakash et al. 2019; Sumanapala & Wolf 2022). Furthermore, after two years of recurring lockdowns and quarantining, people understand better than ever the adverse effects of confinement and the need to go outdoors and move around (Tumi et al. 2021). Having fewer, larger enclosures with mixed species is one way to navigate issues with space (providing that animals are compatible) whilst also creating exhibits that give more opportunities for natural enrichment and even mimic wild habitats (Melfi & Feistner 2002; Mehrkam & Dorey 2015; Chatpongcharoen et al. 2021).

Given long standing issues with space and an ever-growing number of species at risk, whether from habitat loss, (Sumatran rhinos, *Dicerorhinus sumatrensis* and saolas, *Pseudoryx nghetinhensis* (Corlett 2007; Zafir et al. 2011; Nguyen et al. 2022)) hunting (sea turtles and Tasmanian devils, *Sarcophilus harrisii* (Mancini et al. 2011; Pemberton et al. 2019), or climate change and disease (many species of lizard and amphibians (Huey et al. 2010; Diele-Viegas et al. 2020; Neely et al. 2020; Peterson et al. 2020), it is paramount that zoos concentrate on species in need of help whilst reducing numbers of species that do not need help. Thankfully, the propagation of endangered species in captivity need not be forever if conducted alongside reintroduction programmes, which now benefit from a more advanced understanding of reintroduction science and have much higher chances of success than early attempts (see: Tribe & Booth 2003; Soorae 2008; Swaisgood 2010; Conway 2011).

Today, numerous species have enhanced survival chances in the wild thanks to breeding programmes and reintroduction efforts as exemplified by various species including California condors (*Gymnogyps californianus* (Ralls & Ballou 2004)), black-footed ferrets, (*Mustela nigripes* (Jachowski & Lockhart 2009)), whooping cranes, (*Grus americana* (Urbanek et al. 2010)), and wolves (*Canis lupus* (Smith & Bangs 2009)) in America, echo parakeets, (*Psittacula eques* (Tollington et al. 2013)) in Mauritius and kakapos (*Strigops habroptilus* (Jamieson 2015)) and saddlebacks (*Creadion carunculatus* (Taylor et al. 2005)) in New Zealand. Nevertheless, if zoos are to meet their full conservation potential, they must continue to work towards providing better conditions to meet the biological requirements of their animals as well as become reservoirs of rare wildlife (Conway 2011; Keulartz 2015). It has been suggested that zoological institutions; (i) tailor facilities and breeding programs to provide the best conditions for species that are threatened or endangered in the wild, (ii) work collaboratively so that sufficient numbers of animals are kept to meet behavioural needs, genetic viability, and demographic requirements of propagation, (iii) disseminate rare species management and medical care and assist with reintroductions and other conservation efforts and (iv) champion protected wildlife area needs and educate visitors to garner support (Tribe & Booth 2003; Conway 2011; Keulartz 2015; Wildt et al. 2019).

4.5.2 Research expanding the captive care toolbox

Captive animals are known to display atypical behaviours (see: Mason & Latham 2004; Shyne 2006; Clubb & Mason 2007) whilst also lacking other behaviours that are present in wild conspecifics (Mathews et al. 2005). Plenty of studies demonstrate how appropriate environmental enrichment (which often involves introducing natural elements like rocks, twigs, running water and specific plants) can encourage a wider range of neutral-positive behaviours in managed care, reducing or even putting a stop to detrimental stereotyped behaviours (*cf.* Melfi & Feistner 2002; Clubb & Mason 2007; Breton & Barrot 2014; Mehrkam & Dorey 2015; Chatpongcharoen et al. 2021). Whilst it might not make sense or always be beneficial for captive animals to display the same behavioural repertoire as wild conspecifics (Veasey et al. 1996a; Howell & Cheyne 2019), our knowledge of behavioural plasticity and ecology in the wild can be harnessed to improve the quality of life for animals in captivity (Mehrkam & Dorey 2015; Chatpongcharoen et al. 2021). This being the case, it seems likely that knowledge of step length distances could also benefit captive animals by helping inform enclosure size according to species-specific movement behaviour.

Technological advancements also mean that animal behaviour can be analysed at an individual level and used to give an indication of well-being, for example, detecting lameness in dairy cows with leg-mounted accelerometers (Thorup et al. 2015), monitoring heart rate and activity in Koalas in response to tourist proximity (Ropert-Coudert et al. 2009) and providing quantified baseline behavioural data for bottlenose dolphins in human care (Shorter et al. 2017). These studies demonstrate how, in time, welfare assessment methods could be updated and tailored to meet the needs of individuals. This would mark a huge advancement, as generally speaking, welfare assessments have been based on resource-based measures (things like space, lighting and food requirements) and observable, qualitative markers which although useful are not specific to an individual's needs and do not measure internal responses (Whitham & Wielebnowski 2013; Clegg et al. 2015; Salas et al. 2018; Benn et al. 2019).

4.6 Perspectives– important drivers of movement

There are a great many variables that influence animal movement and changes in direction including: resource distribution, obstacles (e.g., bodies of water, rocks and vegetation), social interactions, predators and topography (Hampson et al. 2010a; Shepard et al. 2013; Aini et al. 2015; Richardson et al. 2018). Because animals change direction in response to environmental stimuli (Potts et al. 2018), step length frequency distributions may reflect the distribution of elicitors, which may, in itself have important implications for movement behaviour and well-being given that animals have adapted to their natural environment over thousands, if not millions, of years (Thorpe et al. 2007; Finch et al. 2014; Li et al. 2014; Wu et al. 2014; Rinker et al. 2019).

Both free-living and captive animal movement may often not be dependent on innate behaviour drivers; for example, the daily distance travelled by mountain gorillas differs vastly in response to food availability (Caillaud et al. 2014) and wild animals roam large distances, often travelling for days in order to access water (Hampson et al. 2010a) whereas managed care animals do not. In addition, free-living animals, despite often having large expanses over which to roam, may conduct various types of relatively short random walks, such as in environments where resource locations are unknown (Bartumeus et al. 2005). On the other hand, captive animals which have limited space access are often given enrichment, both structural and nutritional, to encourage activity and to diversify behaviour (Burghardt et al. 1996; Case et al. 2005; Mellor & Beausoleil 2015; Bashaw et al. 2016; Alba et al. 2017; Chatpongcharoen et al. 2021). All of these factors can affect animal movement and are beyond the scope of a single study, particularly because captive and wild environments differ substantially (Zwart 2001).

Still the percentage of wild animal straight-line movement paths that can be undertaken within a managed care environments is important because the effects of low levels of mobility are not fully understood (section 4.3) and may have consequences at a psychological, physiological and musculoskeletal level (Hampson et al. 2010a). Providing enough space within enclosures for a sufficient percentage of step lengths (e.g. 50 % or more) may limit some potential adverse effects of captive environments (Clubb & Mason 2007; Breton & Barrot 2014), however, the ability to provide an adequate amount of space for species with long step lengths is in most cases not possible: to accommodate even 10 % of an Andean condor’s step lengths, aviaries would have to be about 500 m long and to accommodate 50 % they would have to be over 1,800 m long. The largest mixed species aviary, at 223 m in its longest length, would permit just 0.9 % of step lengths. In any case, accommodating such small percentages step lengths is unlikely to meet the movement behaviour requirements of a species, especially ones like Andean condors that typically glide and require added space to manoeuvre (Williams et al. 2020). An understanding of free-living movement, which is the culmination of both innate and external drivers (noting that distinguishing between the two is complicated), can only be useful as both are likely to contribute to an animal's well-being overall.

4.7 Future work

Sensible advancements to the work presented here would be to increase the sample size as mentioned above. Increasing the numbers of wild animals and species for which step lengths exist should be readily achievable as a wide variety of free-living animals have already been fitted with DDs and other motion- and orientation-sensitive tags (Eckert 2002; Wilson et al. 2005; Wilson et al. 2006; Quintana et al. 2007; Brown et al. 2013; Wilson et al. 2018; Gunner et al. 2020; Williams et al. 2020; Wilson et al. 2020; Wilson et al. 2021a; Gómez-Laich et al. 2022). Larger sample sizes would give statistical power, allowing for a more in-depth analysis of straight-line travel. Gathering data from enough individuals per species and location would enable meaningful comparisons to be made regarding the extent to which step length varies among free-living individuals, within and between groups. It would also be useful to deploy DDs on animals maintained in captive enclosures of various sizes and examine their step length distances in relation to those of free-living animals as well as to determine the percentage time spent travelling per day. At the same time, studies in captivity could begin to investigate the consequences of restricting animal movement, for example if the incidence of pacing was related to step length distribution. Ranging behaviour is already known to have implications for a variety of captive care welfare measures, from physical health (Hampson et al. 2010a) to infant mortality (Clubb & Mason 2007). Assessing whether such measures are linked to or increase at a certain proportion of step length restriction might also be very valuable for informing enclosure size.

Whilst recording and analysing free-living movement data is of value to a variety of fields of research such as movement ecology (Ropert-Coudert & Wilson 2005; Nathan et al. 2008; Wilmers et al. 2015), behaviour (Naito 2004; Brown et al. 2013), physiology (Block 2005; Sherub et al. 2017) and conservation (Wilson et al. 2008; Bograd et al. 2010; Wilson et al. 2015), fulfilling the ultimate goals of this work requires cooperation between zoological associations, zoos and aquariums and researchers. Fostering good relationships between these three groups would build trust whilst facilitating the sharing of information and data and working towards shared goals (Hutchins & Smith 2003; Fernandez & Timberlake 2008; Kubarek & Johnson 2022). Indeed, such an approach is essential for studies such as this one to collect enough zoo-dependant data to be meaningful. It would also be necessary in order to implement an index such as *ReMI* alongside existing frameworks.

5. Conclusion

The goals of this study were; (i) to use step lengths to suggest which animals may be more suited to managed care environments and (ii) to create an index, *ReMI*, that could help inform enclosure size to use step lengths to suggest which animals may be more suited to managed care environments. By assessing the percentage of step lengths allowed in captivity, this study attempted to reveal which animals were more likely to have a sufficient amount of room considering the free-living movement behaviour of conspecifics. For six out of nine species considered, less than 3 % of step lengths were realisable within existing enclosure guidelines (for Aldabra giant tortoise and loggerhead turtles over 60% of step lengths were realisable and for whale sharks no guidance on space was provided). In fact, space recommendations for all three bird species (Andean condors, imperial cormorants and Magellanic penguins) were frequently below the smallest recorded step length distance, indicating that current standards for animals operating in a three-dimensional space may not be suited to their movement requirements. By contrast, zoo enclosure sizes for animals with shorter step lengths, like loggerhead turtles, Arabian oryx and Aldabra giant tortoise, allowing between 38.7–98.8 % of step lengths, illustrated how they were afforded relatively more space in captivity.

It is important to recognise that zoos are limited when it comes to space, so animal exhibits are not designed to be as large as possible but to be suitable and stimulating environments that meet captive animal needs. That said, comparing step lengths with enclosure size is of value (and other studies have explored similar themes (Clubb & Mason 2007; Hampson et al. 2010a; Breton & Barrot 2014)) because it may help identify animals whose needs are easier to meet in captivity. In future, investigations looking at whether the incidence of pacing correlates with step length could reveal suitable thresholds (e.g., $ReMI_{CSL\_70\%} = 1$) and facilitate the integration of *ReMI* into comprehensive captive welfare guidelines to help maximise animal well-being in captivity.

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Chapter 7

1. Synopsis

1.1 Coming of PhD age

"As you get older, the questions come down to about two or three. How long? And what do I do with the time I've got left?" – David Bowie

It was many months into my PhD before I realised that I could no longer in good conscience keep telling myself that I was 'just starting out', despite it feeling that way. Learning how to deploy the tags and operate their custom software, complete with raw data channels for accelerometery, magnetometry, temperature and pressure, with features allowing them to be visualised, smoothed and combined giving a variety of derivatives, was daunting to say the least. Moreover, recording several different parameters at 40 Hz, even on a relatively small number of individuals, quickly wracks up a LOT of data, let alone trying to wade through data from over 230 deployments on 64 animals. And despite this sounding like a very decent sample size, the number of turtles suitable for comparison was much lower (see Chapters 2–5) as individuals varied greatly in size (3.2–90 kg, averaging around 20.4 kg) and health status, with a seemingly never-ending list of disparate injuries and a smaller but significant assortment of potential diseases. On top of this, turtles were sometimes housed in twos or threes rather than individually and maintained in indoor and outdoor tanks with differing water capacities. Aside from these confounding factors, there were a number of occasions when water leaked into the devices, batteries ran out, memory cards failed or became corrupted, and tags broke or fell off (read: turtles did their utmost to remove them and succeeded) which further reduced my motley pool of suitable data.

I was particularly underprepared to deal with rehabilitating turtle movement data from tags that, without thorough inspection, appeared homogenous and fairly static in nature. It certainly did not resemble the clear behavioural data published on a variety of species including penguins, cormorants, vultures, badgers, sheep, cows, cheetahs, whale sharks and lemons sharks (Shepard et al. 2008b; Wilson et al. 2008; Walker et al. 2015b). I think that part of the reason why the turtle movement traces lacked diversity was due to rehabilitation tanks being relatively small and shallow (2–6 m in diameter and 0.95 m deep), without much enrichment and because turtles spent large portions of time resting on the tank floor, floating (often orientated towards a filter pipe (*pers. obs*)) or swimming slowly. Further to this, turtles do not typically sit, stand, or jump, (changes in orientation that can be easily picked up *via* tags) rather they tend to lie and swim more or less horizontally, particularly in shallow tanks. After what felt like a few short months, deploying tags and devising potential movement metrics, I found myself in mid-to-late PhD life (the nitty-gritty), with many loose ends in need of tying up and a great deal of analysis and writing pending.

1.2 Into the unknown, embarking on the thesis

Over the course of this PhD, I proposed a variety of movement-based metrics for animal health using data collected *via* motion- and orientation-sensitive tags (Daily Diaries, DDs (Wilson et al. 2008)). These tags record high resolution data at high frequencies and are potentially very powerful tools for assessing numerous aspects of animal behaviour, giving critical data about animals that may not even be observable (Shepard et al. 2008a; Wilson et al. 2008; Shepard et al. 2013; Gunner et al. 2021). Although I found links between certain states of health conditions and movement metrics (Arkwright et al. 2020) and proposed looking at turn extent and angular velocity as well as straight line movement when assessing enclosure dimensions, this type of work is clearly in its initial stages and would benefit from a much larger sample size than I had.

Indeed, the process of defining tag-derived behavioural biomarkers (TDBBs) for health is a lengthy one, requiring multiple animals in comparable states of health or illness. This means that, in my study, I did not have access to sufficient animals to test my hypotheses robustly and given that managed care environments only have small numbers of animals anyway, this problem will continue (Swaisgood & Shepherdson 2005; Kuhar 2006). A global initiative encouraging data sharing and access to animals across institutions may alleviate this issue, especially if supported by major zoological associations such as BIAZA, AZA and WAZA (see Chapter 6). No doubt the lives of vets and animal researchers would be made considerably easier whilst improving the statistical power and robustness of studies. Also, given the number of sensors carried by DDs, and their potential for creating a seemingly infinite number of variables (see previous chapters to exemplify just a few), it would take concerted effort by many individuals to reason their way through the myriad of options that might code for state.

A solution might be to employ artificial intelligence and machine learning to facilitate this (Bidder et al. 2014; Walker et al. 2015a; Valletta et al. 2017; Potts et al. 2018; Wilson et al. 2018; Christin et al. 2019; Turan & Çetin 2019; Chakravarty et al. 2020; Munden et al. 2020). While true to an extent, machines generally only deal with the data they are given: they do not reason their way into considering the value of select metrics. For example, raw data for acceleration can be turned into static and dynamic values (with each of these from each axis meaning different things (Shepard et al. 2008a)) and these can be combined, in pairs or a triplets, vectorially (Qasem et al. 2012) or summed (Wilson et al. 2020), and differentiated (to give jerk (Ydesen et al. 2014)) and represented in a multitude of ways, including across g-spheres (Wilson et al. 2014). Judicious treatment and fusion of parameters therefore seems an almost impossible task, but knowledge of the meaning of sensor outputs combined with some understanding of how study animals actually move in the real world is a first important step towards consideration of what specific outputs might code for animal state. In this, a prime consideration is to document how what we observe typifies animal movement (rotation, change in pitch, roll, linear acceleration etc.) according to their 'state' (a return to Tinbergen (1960, 1963)) and then reasoning how this movement will affect sensor output. Even getting to this stage, however, requires hard work. Still, the ever-growing number of researchers using tags should facilitate progress.

Despite the magnitude of the task, my thesis has endeavored to highlight some of the potential advantages of using tags within a captive setting for welfare purposes, something for which very few studies exist. Of note, is a study that deployed accelerometers in combination with electrocardiogram recorders on koalas to measure heart rate during inactivity in the presence of tourists (Ropert-Coudert et al. 2009) and another study that used motion-sensing tags to examine the activity of bottlenose dolphins under human care to assess their well-being (Shorter et al. 2017). This means that my work may be considered to be one of the first explorations of a few promising avenues of research that might help our understanding of the well-being of captive animals.

This final chapter allows me to ruminate on some of the issues I consider to be important in my quest for TDBBs relating to animal state, health and well-being, whilst also giving me the opportunity to present a few things of interest that I noted in passing but did not pursue within the main chapters of this thesis (often because the sample size was too small to give any sort of statistical robustness). Nonetheless, as with all ‘incidental’ observations, further work may verify my suspected trends, or, my observations could be a useful starting point for future workers undertaking research in this field.

1.3 Constraints and biases

Early on in this work, I hoped to use DDs to define simple metrics that could be used to determine ‘healthy’ turtle behaviour at rehabilitation centres. I looked at movement metrics including activity level, turning, resting, and surfacing events (i.e., breathing rate). Defining ‘healthy’ turtle movement at the Arca del Mar rehabilitation centre had the added complication that most individuals had been bycaught and were recovering from various injuries (some of which were undetectable without imaging studies). Those that were admitted without any signs of disease or injury were considered to be ‘healthy’. Regardless of health status, animals held at the Arca del Mar facility had frequent contact with humans both from veterinary staff and guided tours given to the public as well as feeding and tank cleaning, all factors that can affect movement behaviours.

Human contact was even higher in summer due to increased visitors: on one occasion I found a class of excitable summer school kids standing all around a tank, gleefully throwing chunks of food to a turtle I had tagged. Another time, when glancing over raw movement data I saw that a turtle had been highly active in the early hours of the morning (3:00–4:30 am; Figure 1); what may have caused this unusual activity is unknown– perhaps a light came on, maybe there was a loud noise, or a security guard was doing the rounds… All turtles in captive care are likely to be subject to similar disruptions which means that either TDBBs need to be robust enough for such disruptions not to matter or cameras need to be installed so that ‘disruption events’ can be excluded from the data.

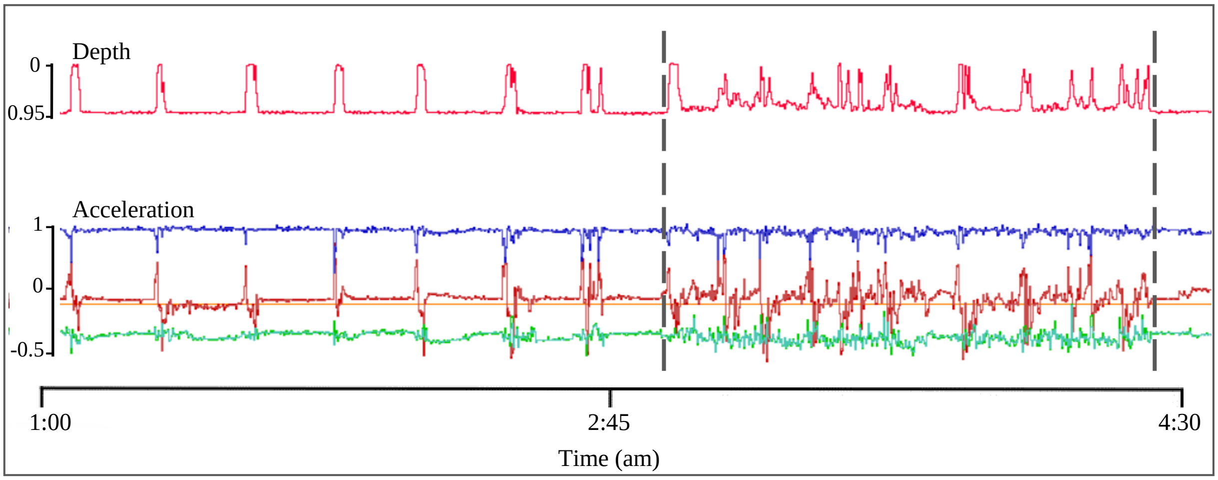


Figure 1. Depth (0–0.95 m) and tri-axial acceleration (g) traces from a turtle (T380) tagged in a rescue centre tank on 16/03/18. Between 1:00–3:00 am the turtle surfaces to breathe roughly every 15 minutes (illustrated by peaks in depth trace and increased amplitude in acceleration traces) and returns to resting on the tank floor (illustrated by flat trace lines); this regular behaviour ceases around 3:00 am and is followed by approximately 80 mins of higher activity (see depth and acceleration traces between dotted vertical lines).

In order to augment numbers of ‘healthy’ animals, four adult-sized turtles that had been head-started at the Taliarte rescue centre, Grand Canary Island, were also tagged. Unlike the turtles at the Arca del Mar centre, these individuals were held in outdoor rescue centre tanks with some shading and received less human interference and it was because of this that I was interested to see whether changes in behaviour coincided with diurnal light and temperature changes. By visualizing the data in different ways and appreciating that I still only had a sample size of four animals, I noted an apparent decreased incidence of turning at night and increased turning in line with rising water temperature and daylight hours (Figure 2a, b). Against this, fluctuations in VeDBA throughout the day were minor (Figure 2c), showing the limitations of this activity metric for slow moving, gliding species (Wyneken 1997; Eckert 2002; Wilson et al. 2019). However, all individuals except ‘Hulk’, (the largest individual at 66.4 kg whilst the others ranged from 42.6–47.9), generally displayed increased VeDBA at higher water temperatures (temperature varied between 20.1–30.3°C; Figure 3a) and water temperature has been found to affect sea turtle behaviour (Storch et al. 2005). Contrary to this, I noted that there appeared to be no relationship

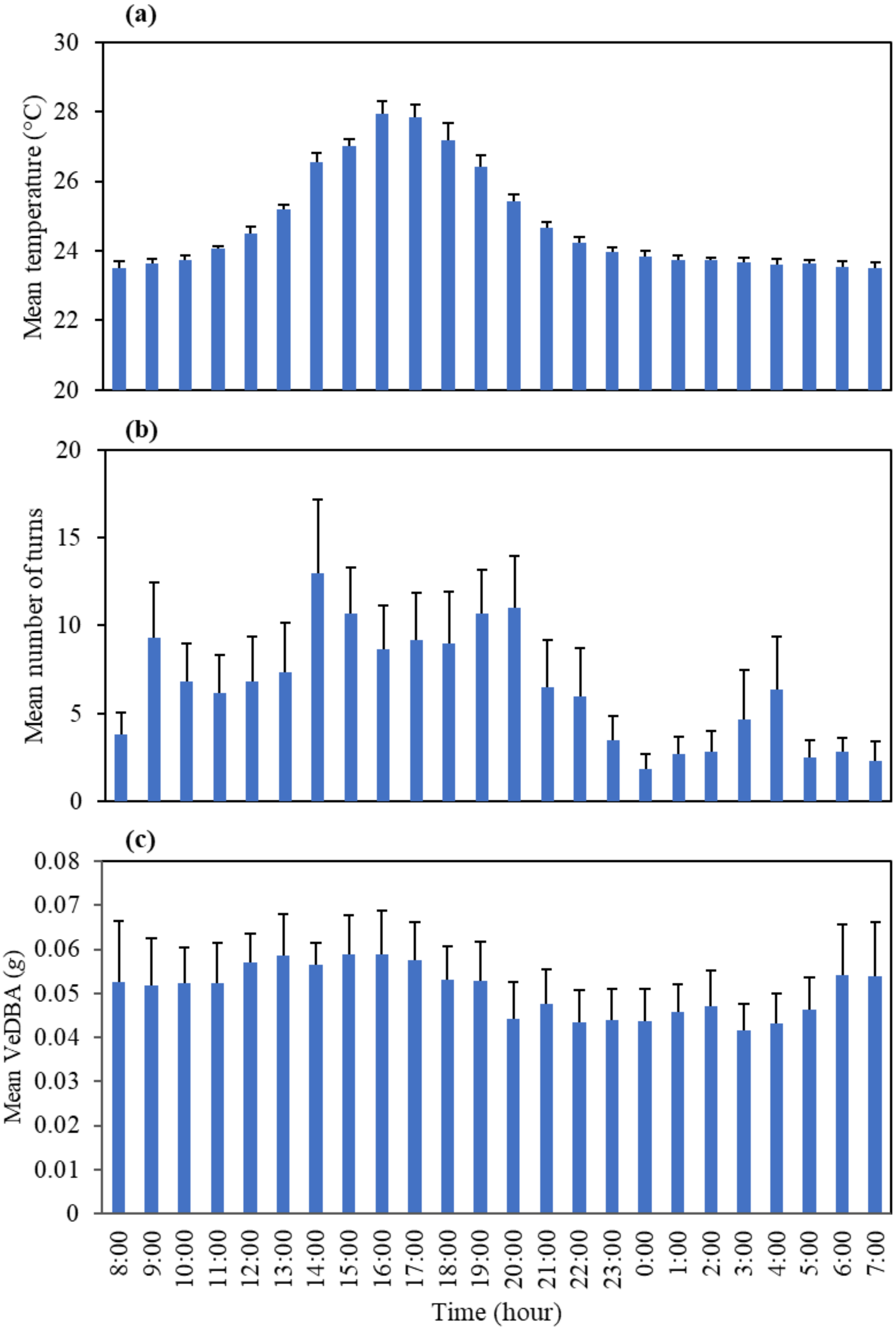


Figure 2. Data from four turtles in outdoor tanks at the Taliarte rescue centre, Grand Canary Island, during the first 24 hours of tag attachment. Hourly means and standard error bars are calculated for: (a) tank water temperature (°C), (b) number 360° turns performed by turtles and (c) VeDBA (g). Note slightly increased turning and VeDBA between ~12:00–20:00 in line with higher water temperatures and daylight hours (sunrise,~8:00 am; sunset ~20:00 pm).

between VeDBA and temperature for animals at the Arca del Mar facility, possibly because the temperature varied much less and did not get as hot (21.6–25.8°C; Figure 3b).

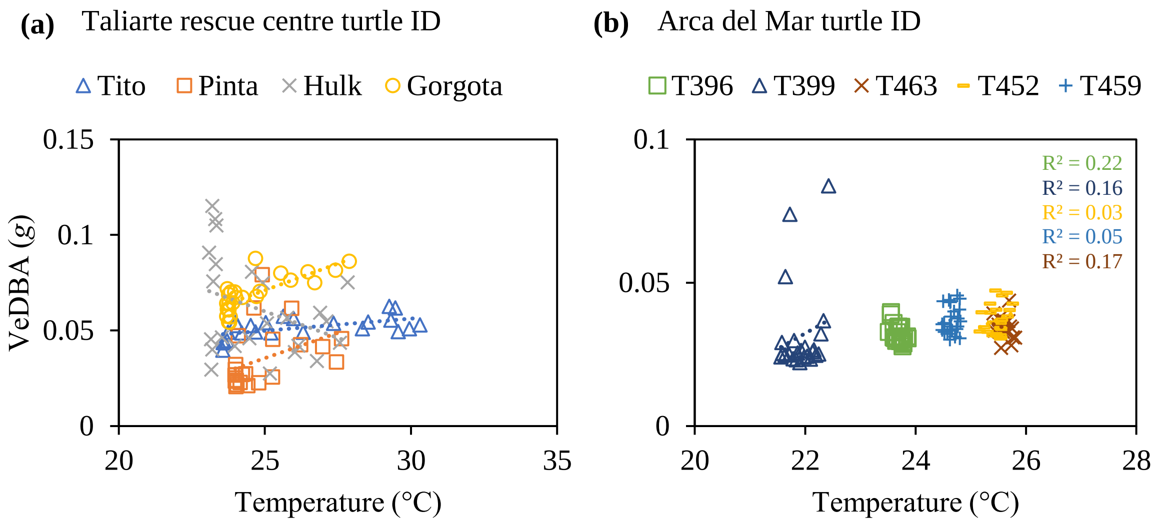


Figure 3. Mean water temperature (°C) per hour over a 24-hour period for turtles in tagged at (a) the Taliarte rescue centre, Grand Canary Island (n = 4) and (b) the Arca del Mar rehabilitation centre, Valencia (n = 5). Note: both y- and x-axes are on different scales; R^2 *values are coloured and ordered according to the legend. At the Taliarte centre VeDBA generally increased with temperature for all individuals except Hulk; at the Arca del Mar centre VeDBA appeared to be unaffected by temperature, however temperature varied much less.*

Comparisons between turtles at both rehabilitation centres showed that those at the Taliarte rehabilitation centre typically had a much higher number of turns per hour recorded at 45° and 180° thresholds with the linear relationship between turn extent and VeDBA decreasing with increasing angle (Figure 4a, b *cf*. c, d and R^2 values). The highest numbers of 45° turns recorded for turtles at the Taliarte centre were roughly four times higher (or more) than turtles at Arca del Mar (Figure 4a, b). This divergence was a little less pronounced for turns of 180° mainly because one small turtle (T399, weighing 5.7 kg) at the Arca del Mar facility completed a similar number of turns to individuals in Taliarte (Figure 4c, d). These differences may be attributable to multiple factors: a notable differentiation between the groups was that the turtles at the Taliarte centre were adults (weighing 50 kg ± 11.2 SD), unlike those at the Arca del Mar centre that were juveniles and sub-adults (weighing 10.3 kg ± 7.3 SD)– the former group had also been head-started whilst the second had been ‘wild caught’ and it could be that these contrasting life histories had profound effects on behaviour.

Another clear distinction was that the animals in Taliarte were in outdoor tanks and were much more exposed to the elements, resulting in a more variable water temperature and no doubt light changes as well. Conversely, the individuals at the Arca del Mar centre were housed in tanks in a semi-enclosed building with both natural and controlled lighting; this shielded and regulated environment may have induced low levels of activity. However, both groups were housed in simple rescue centre tanks, without any structural enrichment so from that point of view the environments were similar. At the Taliarte centre, Hulk and Pinta were maintained in larger tanks with an available water mass of 10,000 L and the other two slightly smaller individuals were maintained in tanks with an available water mass of 4,000 L. Four turtles at the Arca del Mar facility were held in semi-circular tanks with a water capacity of 3,500 L, and the largest individual, 396 (22 kg) was held in a semi-circular tank with a water capacity of 6,100 L. Based on visual inspection of the data, there appeared to be no clear increase or decrease in turning behaviour associated with turtle weight and/ or tank size, but this sample size is small. It is worth noting, however, that statistical analysis in Chapters 2 and 3 also found no significant relationship between turtle weight, tank size and turning.

Aside from differing life histories it is also possible that tank shape itself affected turning behaviour, with the circular tanks at Taliarte giving rise to a hugely increased number of turns per hour, perhaps through inducing patterned swimming in a figure eight or around the perimeter of the tank. In contrast, the corners of the semi-circular tanks at the Arca del Mar facility provided an obvious resting point (*pers. obs*). Within aquariums a variety of mechanisms are used to interrupt repetitive swimming patterns like swimming around the perimeter of a tank: types of enrichment include PVC piping, floating barrels, buoys, vinyl and bubble curtains (Schreiber & Coco 2017).

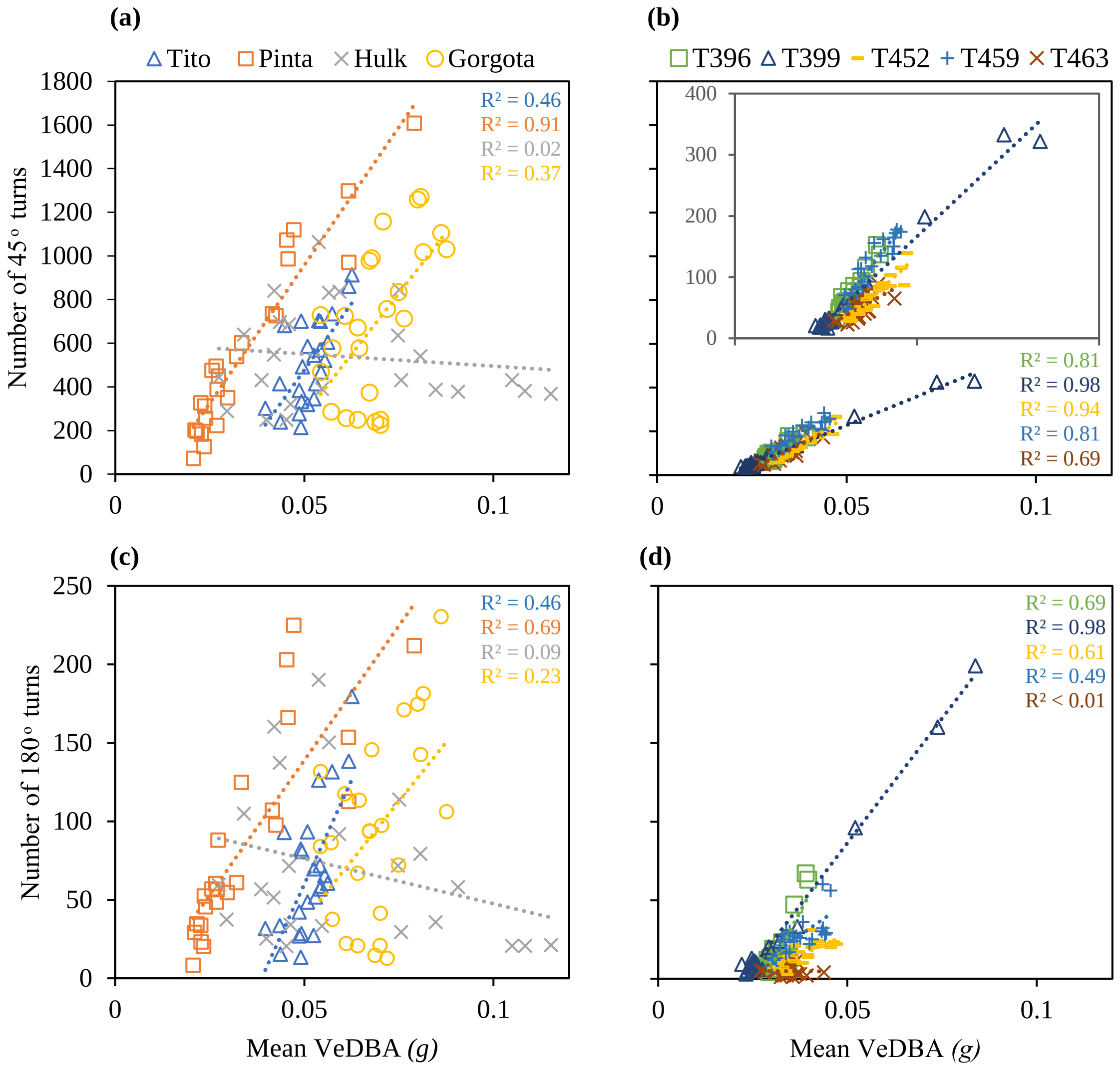


Figure 4. Total number of turns per hour over a 24-hour period that equalled or surpassed (a, b) 45°, and (c, d) 180° for turtles in tagged at the Taliarte rescue centre, Grand Canary Island (n = 4; left-hand side) and the Arca del Mar rehabilitation centre, Valencia (n = 5; right-hand side) against mean VeDBA. Y-axes for turn angles of the same extent are on the same scale and all x-axes are graphed on the same VeDBA scale for ease of comparison; R^2 values are coloured and ordered according to the legend. For individuals of both groups (except Hulk), VeDBA generally increased with number of turns recorded, especially 45° turns; this relationship was stronger for turtles at the Arca del Mar rehabilitation centre (which typically had higher R^2 values) although the total number of turns completed was much higher for turtles at the Taliarte centre.

Given that the difference in turn rate is so stark, I wonder if there might have been some magnetic interference at the Taliarte rescue centre that resulted in extra turns being recorded. unfortunately, not being on site, I was unable to check if this was the case. Due to the differences in 'healthy' turtle behaviour at both centres, I only used data from turtles at the Arca del Mar rehabilitation centre when comparing healthy turtles with individuals recovering from gas emboli (Chapters 2 and 3). I focused my analysis on movement metrics that showed most promise when differentiating between healthy and recovering turtles such as variance in body attitude (i.e., pitch and roll values), the number of 45° turns and the mean angular velocity per hour.

Another issue with tagging turtles in small rescue centre tanks was that turtles could not swim as they would in large exhibits or in the wild, which made flipper beats hard to define. This along with inter-individual variability, small sample sizes and no clear-cut differences between healthy turtles and individuals recovering from gas emboli, meant that I was unable to come up with a healthy turtle flipper beat signature for animals in rescue centre tanks.

Whilst pursuing a similar train of thought, I began looking at prey signatures– where head movements may be used to identify the prey types being eaten. For example, a study deploying mandibular sensors on different species of penguins was able to identify various behaviours including ingestion, breathing, calling, head shaking and preening (Wilson et al. 2002). In this study, captive feeding trials revealed that prey mass could also be calculated with a relatively high degree of accuracy ($R^2 = 0.92$), and that changes in beak angle over time could be used to allude to prey type, the two combined giving an indication of different prey types (Wilson et al. 2002). Given these findings, I was interested to see if head mounted tags with accelerometers and magnetometers (Figure 5) could be used to identify what prey type a turtle was eating. I investigated this in conjunction with feeding trials with motile or sessile prey types that were conducted to see if different prey types elicited different behavioural responses in sea turtles (Chapter 4).

Figure 5. Loggerhead turtle in a rescue centre tank with a head tag and a carapace tag; both tags are DDs and are attached using a two-part epoxy.

Visualisations of head movement data using a g-sphere approach (Wilson et al. 2016) based on acceleration during feeding events with clams and crabs revealed similar VeDBA traces (Figures 6 and 7), mirroring results from carapace tag data in Chapter 4 where VeDBA did not differ significantly with prey type. The only apparent dissimilarity in VeDBA values occurred during a limited number of clam feeding events with very low VeDBAs recorded when the pitch angle was below the equator line (Figure 7b, feeding events 3 and 4). This indicated that the turtle was practically stationary, approaching the clam from above, with its head pitched down almost vertically (pitch > 90°). In contrast, crab feeding events usually occurred close to the north pole of a g-sphere (pitch 0°) indicating that the turtle was interacting with the crab at distance, with no points occurring below equatorial line (pitch 90°) in three out of four feeding events (Figure 7a, crab feeding events 1–3). Although visualizations did on the whole indicate that clam feeding events typically occurred over a wider pitch angle, this finding was not consistent (*cf.* Figure 7a, crab feeding event 4 and Figure 7b, clam feeding event 1, that occurred over a similar range of pitch angles).

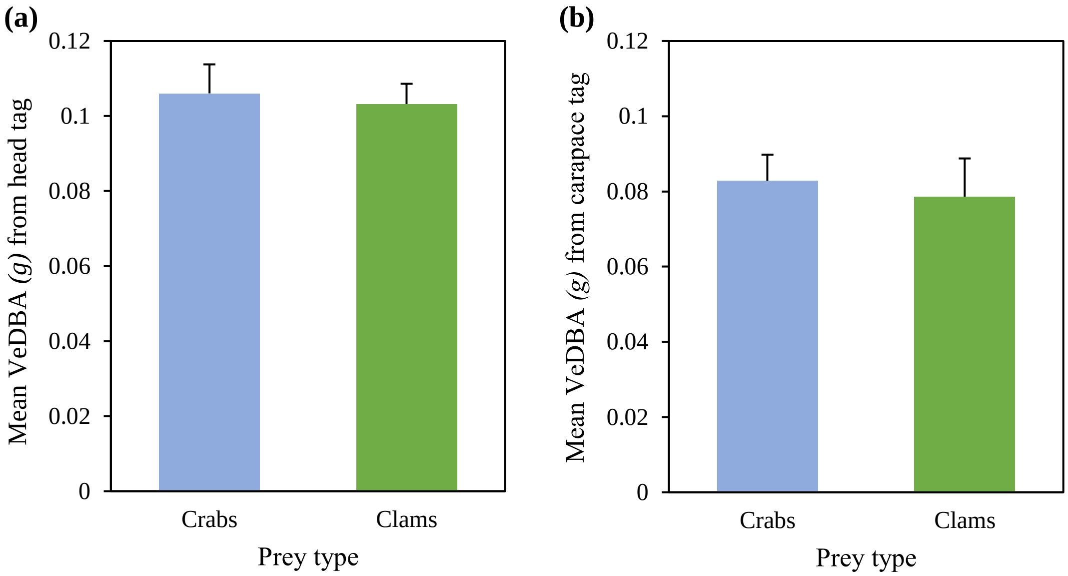
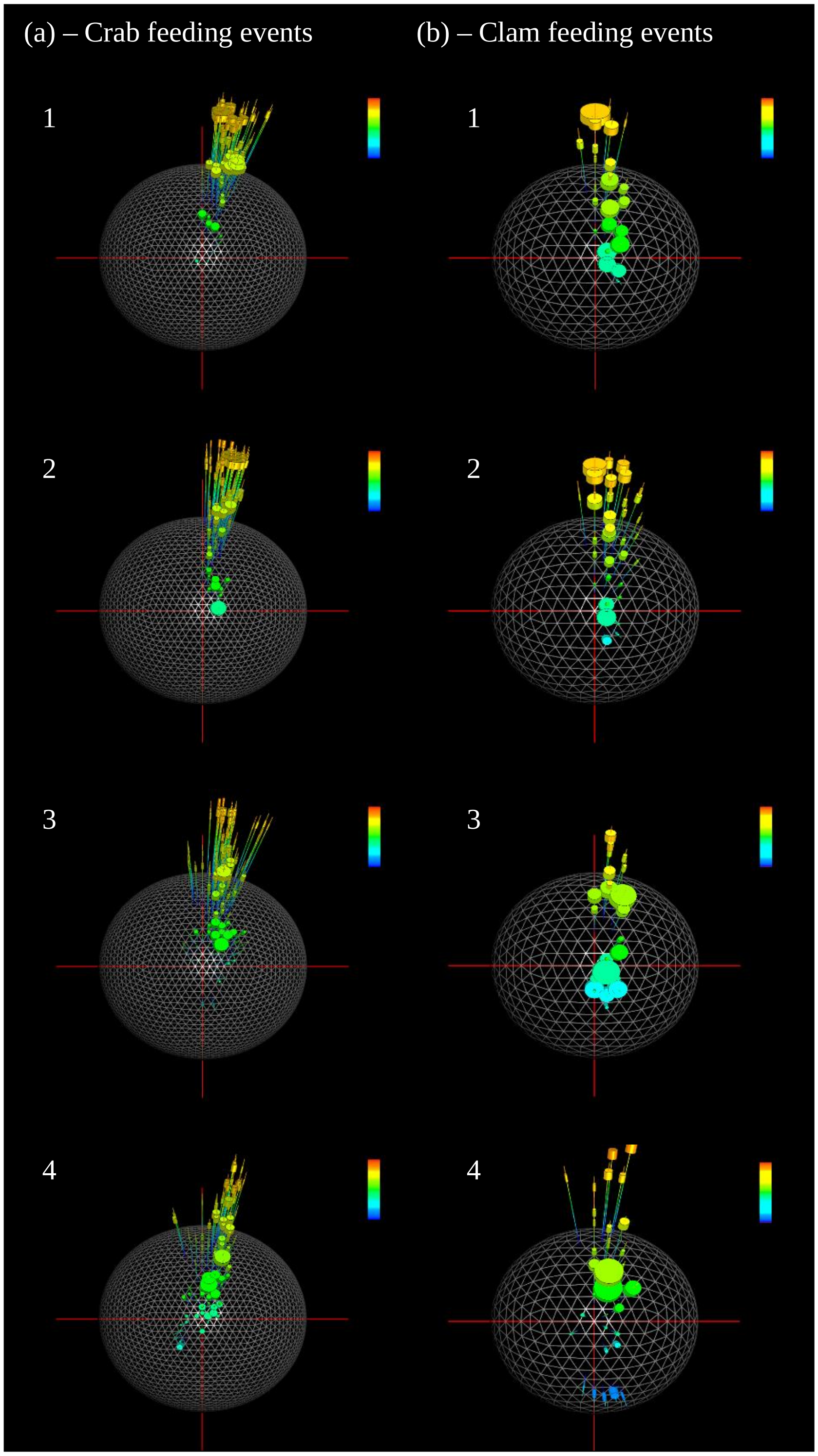


Figure 6. Mean VeDBA (g) from (a) head tags and (b) carapace tags (daily diaries, DDs) recorded during feeding events with crabs and clams. Error bars show standard error. Crab feeding trials were conducted with ten turtles and clam feeding trials were conducted with eight turtles. Similar mean VeDBAs were recorded for both crab and clam feeding events (although slightly higher for crabs) and for head tags and body tags. N.B. Two of the turtles included had sustained carapace traumas which impaired their mobility resulting in marginally higher VeDBAs (never more than 0.04 g); they have been retained because both individuals took part in both types of trial and to augment sample size.

Interestingly, the feeding duration for crabs was half that of clams (23 s ± 5.7 SD and 47 s ± 18.3 SD respectively) because turtles often took several attempts to break the clams shell and spent much longer eating shell fragments. This preliminary exploratory analysis illustrates some key differences between crab and clam feeding events but with data from only 10 individuals (and various confounding factors– turtle weight, health, tank size and various disruptions from tank cleaning to visitor presence), there is not enough data for robust statistical analysis.

Figure 7. Spherical plot visualisations of acceleration data ('urchin plots') (Wilson et al. 2016) taken from turtle, T384 (see Chapter 3, Table 1) fitted with a head tag during 4 feeding events each for (a) crabs and (b) clams. Plots show head pitch (from the 'North pole' down to the farthest points below the equator), roll (from the 'North pole' down to the left and right equator points– note that there is virtually no head roll exhibited by the turtles) and VeDBA per pitch/roll angle placed into bins denoted by coloured discs. Disc diameter indicates the number of data points within that bin and increasing distance from the sphere denotes increasing VeDBA. The highest VeDBA values are also indicated by warmer colours (red) and the smallest VeDBAs by cold ones (blue). Note how the distribution of colours is similar in both crab and clam feeding events although the latter typically occur over a greater pitch angle.



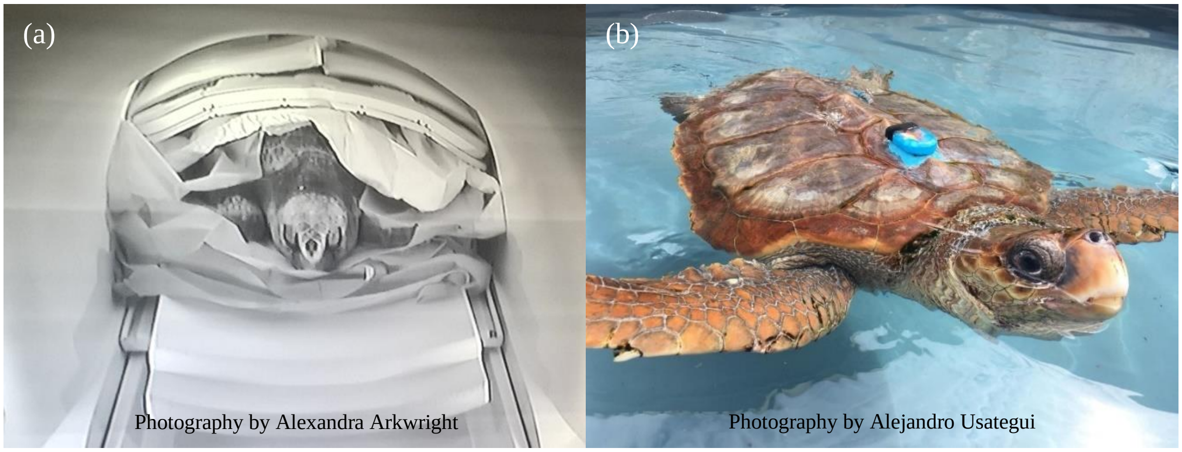
1.4 Animal navigation and magnetism

“Just keep swimming” – Dory, Finding Nemo

A great number of marine species, including salmon and sea turtles disperse across vast expanses of ocean before returning to their natal areas as adults in order to reproduce (Dittman & Quinn 1996; Lohmann et al. 1999; Lohmann & Lohmann 2019). For example, species of salmon including coho (*Oncorhynchus kisutch*), sockeye (*Oncorhynchus nerka*), and chinook (*Oncorhynchus tschawytscha*) return to affluents of the Columbia River in Washington state to spawn after 3 years at sea (Bigler et al. 1996; Dittman & Quinn 1996; Bett & Hinch 2015). In addition, young loggerhead turtles are known to undertake complex migratory pathways across entire ocean basins and back (Bowen et al. 2004), while Kemp’s ridleys and green turtles may travel hundreds or thousands of kilometers away from their natal beaches during their oceanic phase (Lutz et al. 2002; Luschi et al. 2003; Hays et al. 2020). Turtles also repeatedly return to specific foraging grounds following (up to 10,000 km) migrations to nesting sites, a pattern that has been found to continue across several decades (Shimada et al. 2019). This remarkable natal homing ability, across indistinctive swathes of ocean, sometimes after years, a decade or even longer, has remained enigmatic (Lohmann et al. 2008b; Lohmann & Lohmann 2019).

As it stands, this navigational capacity is considered to be the product of two different systems working in tandem: the first system, by way of geomagnetic cues, guides animals over long distances to the general vicinity of the natal area (Lohmann et al. 2008a; Lohmann & Lohmann 2019), then the second system, through use of non-magnetic local cues, (including submerged banks and islands (Hays et al. 2020)) guides the animals to a more precise location (although the level of precision varies considerably between species and populations (Meylan et al. 1990; Avise & Hamrick 1996; Bowen & Karl 2007; Hays et al. 2020)). These long-distance migrations to the vicinity of nesting grounds can be explained by the ability of turtles to utilise variations in the Earth’s magnetic field as a kind of magnetic positioning system or ‘magnetic map’ (Lohmann et al. 2004; Lohmann et al. 2007). Specifically, sea turtles derive positional information from two magnetic elements, inclination angle (Lohmann & Lohmann 1994) and intensity (Lohmann & Lohmann 1996), that vary predictably across the globe giving rise to unique magnetic signatures at different geographical areas (Lohmann et al. 2001). The cues guiding the second homing system in sea turtles remain unknown, species such as salmon, however, are known to use local chemical cues to identify their natal rivers (Lohmann & Lohmann 2019).

Despite the evidence that sea turtles rely on geomagnetic cues to navigate and reach specific nesting and feeding sites (Lohmann et al. 2004; Putman et al. 2011), sea turtles in rehabilitation centres are regularly sent for MRI scans (Gasau & Ninou 2000; Croft et al. 2004; Valente et al. 2006; Arencibia et al. 2012) which expose animals to intense magnetic fields in order to generate high quality diagnostic images, superior to those of radiographs and ultrasound (Walzer et al. 2003; Jandial et al. 2005; Thornton et al. 2005). To date, there are no published studies investigating whether exposing turtles to such intense magnetic fields, (typically pulses at 15,000 G, when the Earth's magnetic field ranges between 0.25–0.65 G, for 1–2 hours (*pers. obs*)), has any transient effects on behaviour or if it could affect their navigational capacities post release. In an attempt to investigate this, I began tagging turtles that were being sent for MRIs prior to and following the scans (Figure 8).



Photography by Alexandra Arkwright

Photography by Alejandro Usategui

Figure 8. Loggerhead turtles in (a) an MRI scanner and (b) in a rescue centre tank with a Daily Diary tag (DD) attached to the second central scute of its carapace using a two-part epoxy.

The turtles that were sent for MRIs had been admitted with gas emboli and the scans were done to see if the emboli had caused any visible damage. Initially, I presented data from a single turtle (T383, see Chapter 2) that had been admitted with moderate gas emboli and found that directionality, i.e., the amount of time devoted to a particular orientation, increased in the days following the scan (Figure 9).

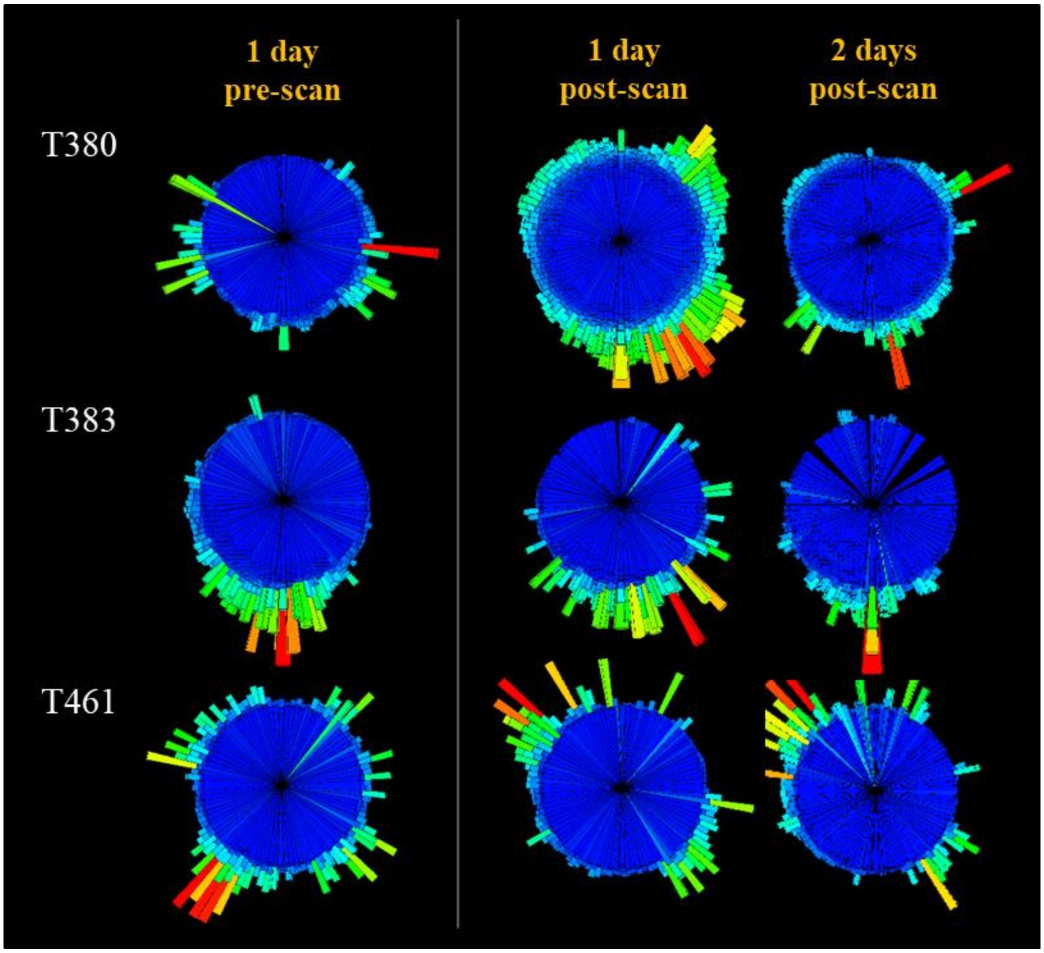


Figure 9. Body orientation histograms (rose plots) representing 24-hour time-periods for three turtles (see Chapter 2, Table 1) tagged one day prior to undergoing an MRI scan and for 2 days following. Bar length indicates the amount of time allocated to a particular direction (the mode is depicted in red). Note how the variability in orientation appears to decrease on the second day after the scan for animals T380 and T383 but not T461.

In order to obtain a better idea of potential transient effects of MRI or if this behavioural change could be attributed to recovering from gas emboli or another factor, I planned to tag turtles both with and without gas emboli following exposure to MRI scans. Unfortunately, resource and time limitations along with a pandemic to boot, did not allow for this. It only adds insult to injury that out of six turtles tagged pre- and post-MRI, two tags failed, and another got water ingress (Murphy's Law (Chew et al. 1991)). In the end, just three turtles recovering from gas emboli were successfully tagged before and after MRI (Figure 9), scans taking 105 mins ± 27.2 (SD) to complete. Two of the three turtle visualizations possibly indicate increased directionality on the second day following the scan which could indicate transient MRI effects lasting up to a day, but this is obviously inconclusive. Aside from having a decent sample size, further study should control for the extent of gas emboli and, critically, the extent of high magnetic field intensity to which the animals are exposed (larger animals are exposed to the magnetic field for longer).

1.5 Brain lateralization and turning

In Chapter five I deployed DDs in order to assess the extent to which captive and wild-type behaviours overlapped during the 'bottom phase' of dives, to see whether it was pertinent to make inferences about 'wild-type' behaviours based on the assessment of turtle behaviour in managed care. Specifically, I compared the behaviour of 'healthy' loggerhead turtles in two managed care settings (rescue centre tanks and structurally diverse aquarium exhibits) with free-living loggerhead turtles. My results revealed significant differences between managed care and free-living turtles in terms of pitch variance, heading variance, absolute angular velocity (AAV) variance and turn extent but not VeDBA. Interestingly, both the variance in AAV and the total number of turns per hour were significantly higher in exhibit turtles than free-living turtles, supporting my initial hypothesis that turtles in more complex environments would exhibit increased rotation as a result of scanning their environment. However, turtles in barren rescue tanks also had a significantly higher AAV and turn rate than free-living turtles. Given these findings I was interested to see whether the ratio of left- to right-hand turns might also differ with environment. My theory being that tank shape, dimensions and enrichment might influence the direction of turns as well as the number of turns. However, I found no evidence to support this as data visualisation revealed very similar ratios of left- to right-hand turns between the three scenarios (Figure 10). The most interesting finding was that all turtles exhibited a clear preference for right turns at higher turn extents (Figure 10c, d).

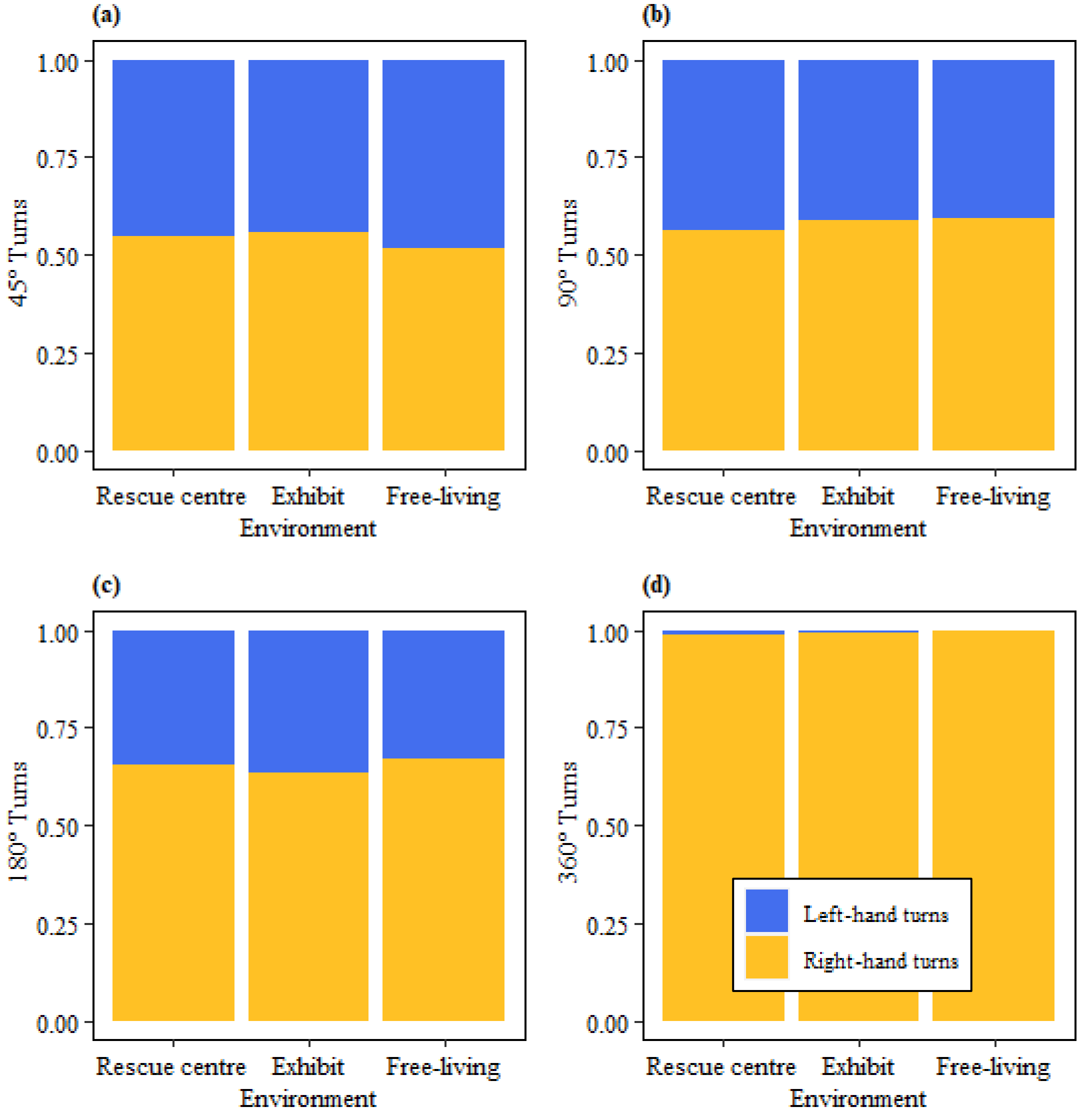


Figure 10. Total number of turns per hour over a 24-hour period for turtles in tagged in rescue centre tanks (n = 10), aquarium exhibits (n = 3) and free-living turtles tagged in the wild (n = 5). Stacked bar charts show the percentage of left- and right-hand (depicted in blue and yellow respectively) turns that equaled or surpassed (a) 45°, (b) 90°, (c) 180° and (d) 360° during 24 hours of 'bottom time' tag data added sequentially. There appeared to be no difference in the ratio of left- to right-hand turns between the three groups.

Although brain lateralization and the evolution of handedness in lower vertebrates has only been studied in recent decades, it appears that turtles are generally right-flippered (Sieg et al. 2010), i.e., their back right flipper is dominant, resulting in a preference for turning to the right. Laterality has been found in a variety of reptiles (Bisazza et al. 1998; Smith et al. 2017; Pellitteri-Rosa & Gazzola 2018; Pellitteri-Rosa et al. 2020) and has obvious advantages when escaping predators as the dominance of one hemisphere prevents the simultaneous activation of contrasting responses (Pellitteri-Rosa & Gazzola 2018). One study found that two species of freshwater turtle (*Terrapene carolina* and *Trachemys scripta*) accumulated injuries on their right side and hypothesised that the turtles; (i) experience right-handed motor lateralization which could affect turning behaviour (Rogers 2002) and (ii) respond more quickly to danger coming from the left, as images are processed with the right hemisphere, making them more susceptible to threats approaching on the right (Lippolis et al. 2002).

1.6 Future courses of action

“To plant a garden is to believe in tomorrow.” – Audrey Hepburn

Obvious further developments to the work presented in this PhD would be to fit more turtles with DDs especially if individuals fit into clear-cut categories, i.e., ‘healthy’ or suffering from gas emboli, carapace trauma and flipper injury. The movement behaviour of these individuals could then be monitored in response to the same stimuli, keeping tank settings as similar as possible in order to minimize confounding factors. Alongside tracking movement behaviour during recovery, monitoring blood biochemistry may also be worthwhile as alterations in various blood markers have been associated with a decline in health status (Snoddy et al. 2009; Melvin et al. 2021). Specifically, I would have liked to have measured corticosterone levels, phagocytosis and lymphocyte proliferation but I was unable to obtain funding for this.

Ideally rehabilitated animals would also be tagged upon release in order to assess survival chances upon reintroduction, although this is costly and unfortunately rarely done. One way of increasing the likelihood of recovering tags at least would be to tag animals in nearshore holding pens which would give individuals time to acclimatize and encourage wild-type behaviour. Unfortunately, despite trying, the Oceanogràfic aquarium was never granted the permit to attempt this.

The use of TDBBs could also prove useful for other bycaught species such as cetaceans and pinnipeds with more complex behavioural repertoires. These species may also exhibit 'healthy' and 'unhealthy' behaviours that are more distinct, making TDBBs easier to define. Additionally, some of the movement metrics proposed in this work could be adapted for animals in managed care environments in the same way that farm animal welfare assessments have been modified for zoos (Fraser 2009; Hill & Broom 2009; Benn et al. 2019) and aquariums (Clegg et al. 2015). Logging technology could transform the study of animal well-being in human care (Ropert-Coudert et al. 2009; Thorup et al. 2015; Shorter et al. 2017) as it has in the fields of animal physiology (Block 2005; Sherub et al. 2017), behaviour (Naito 2004; Whitney et al. 2010; Brown et al. 2013; Whitney et al. 2016) and ecology (Ropert-Coudert & Wilson 2005; Nathan et al. 2008; Wilmers et al. 2015).

Indeed, the use of motion- and orientation-sensitive tags to collect behavioural information from free-living and captive conspecifics could be done with a view to; (i) defining expected behaviours/behavioural states and activity levels and (ii) creating environments that elicit desired behaviours and appropriate levels of activity to help ensure their welfare. Part of creating suitable environments for captive care animals is making sure they are of an adequate size by understanding movement requirements. Animal-attached technologies are ideal for this, and I show how easily movement data can be incorporated into straightforward frameworks (such as *ReMI*) giving evidence-based enclosure size guidance. Considering that the maintenance of animals in captivity, especially that of higher vertebrates, is frequently under scrutiny, objective measures of animal welfare and well-being could prove valuable husbandry tools.

1.7 On a final note

"It's OK to have your eggs in one basket as long as you control what happens to that basket."
– Elon Musk

"It's not OK if the 'basket' is a tag attached to a wild animal, albeit a fairly placid one." *– Me*

The primal concept for this thesis was to investigate the use of motion- and orientation-sensitive tags in a managed care setting, something that has only been done on a handful of occasions (*cf.* Ropert-Coudert et al. 2009; Thorup et al. 2015; Shorter et al. 2017). This emerging field of research has the potential to hone our understanding of captive animal needs, behaviour and welfare through quantifiable metrics. Moving forwards, collaborations between research and zoological institutions offer a marvellous opportunity to grow this field. I feel privileged to have experienced this, working with the Swansea Animal Movement Lab (SLAM) and the research department at the Oceanogràfic aquarium. In an ideal world, a less naïve person (me!) would have covered more ground and presented more concrete findings, especially with regards to TDBBs, to which I devoted a large portion of my PhD life. Perhaps if I had moved onto other topics, such as movement signatures from physical injuries or further explored the effects of physical enrichment, I would have more specific results to present regarding tags and animal welfare. However, that would have prevented me from exploring all sorts of potentially viable movement metrics and analyses (see Chapter 2) that might prove more fruitful under different settings or for other species and, at the very least, should save others some time searching. Hopefully this work presents some useful movement metrics for those looking to use tags in managed care environments and concepts to add to the mix (*cf.* Wilson et al. 2008; Walker et al. 2015b; Wilson et al. 2016; Shorter et al. 2017; Gunner et al. 2020).

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Appendix A (Chapter 2)

Table A1. Summary of tagged turtles including turtle identification number, bycatch origin, weight (kg), curved carapace length (CCL), curved carapace width (CCW), cause of injury/disease (when known) and the animal's state of health upon entry and on the date of tagging (as deduced via veterinary examination). NB: gas emboli (GE) was categorised as mild, moderate or severe; turtles that entered with GE were considered 'convalescent' when tagged within a couple of days of admission as they were only released into holding tanks following hyperbaric chamber treatment and once there was no sign of GE in the blood.

Turtle ID	**Origin**	**Weight (kg)**	**CCL (cm)**	**CCW (cm)**	**Cause of injury/ disease**	**State of health upon entry**	**Tagging date**	**State of health when tagged**
297	Cullera	5.4	33.4	30.5	Trawl/ bottom fishing	Severe GE, died and was resuscitated	17/04/17	Healthy
308	Calpe	10	41.6	39	Trawl/ bottom fishing	Moderate GE	18/04/17	Healthy
318	Cullera	3.5	30	27.4	Trawl/ bottom fishing	Moderate GE	18/04/17	Healthy
320	Peniscola	9.47	39.6	38.2	Trawl/ bottom fishing	Mild-Moderate GE	18/04/17	Healthy
322	Peniscola	5.55	34.4	32.2	Trammel net	Drowned, died and was resuscitated	18/04/17	Healthy
324	Valencia	17	51	46.6	Trawl/ bottom fishing	Healthy	29/04/17	Healthy
325	Valencia	11.54	39.2	37	Trawl/ bottom fishing	Healthy	22/04/17	Healthy
326	Gandia	15.5	46.5	43	Trammel net	Drowned, died and was resuscitated	25/04/17	Convalescent
330	Oropesa	5.6	36	33	Unknown (found floating at surface)	Healthy	22/04/17	Healthy
331	Gandia	3.07	29	26	Trammel net	Intestinal gas, buoyancy issues	22/04/17	Buoyancy issues
332	San Sebastian	18.9	-	-	Unknown (transferred from another aquarium)	Multi-organ failure	29/04/17	Multi-organ failure
339	Benidorm	4.2	34.4	31.8	Stranded with gillnet associated injuries	Severely damaged and infected right front flipper	29/11/17	Damaged and infected right front flipper
342	Vinaroz	15.8	48.5	46	Trawl/ bottom fishing	Severe carapace trauma and damage to spinal cord	15/12/17	Severe carapace trauma and damage to spinal cord
343	San Sebastian	11.19	46.5	39	Unknown (transferred from another aquarium)	Buoyancy issues	15/12/17	Buoyancy issues

344	Vinaroz	12.1	46.6	42.4	Trammel net	Healthy	29/11/17	Healthy
345	Vinaroz	17.1	54	47.2	Trammel net	Healthy	29/11/17	Healthy
347	Murcia	4.52	32.5	31	Unknown, found stranded (transferred from another aquarium)	Carapace trauma, partial front flipper amputation	24/05/18	Carapace trauma, partial front flipper amputation
350	Peniscola	15	50	45	Trawl/ bottom fishing	Moderate GE	29/11/17	Convalescent
352	Cullera	4.45	30.5	29	Trawl/ bottom fishing	Severe GE, died and was resuscitated	07/12/17	Bites and skin infection
359	Benicarlo	20.8	52	50	Trawl/ bottom fishing	Moderate GE	03/01/18	Convalescent
362	Cullera	13	46	42	Trawl/ bottom fishing	Moderate GE	09/02/18	Healthy
380	Calpe	8.4	38.5	37	Trawl/ bottom fishing	Moderate GE	12/03/18	Convalescent
383	Cullera	11.6	44	40	Trawl/ bottom fishing	Moderate GE	15/03/18	Convalescent
384	El Saler	15.2	50	44	Trawl/ bottom fishing	Mild GE	16/03/18	Convalescent
385	Valencia	8.6	40.7	38.6	Trawl/ bottom fishing	Healthy	15/06/18	Healthy
393	El Saler	28.71	60	56	Trawl/ bottom fishing	Moderate GE	18/04/18	Convalescent
396	Vinaroz	22	59	49	Trawl/ bottom fishing	Healthy	08/05/18	Healthy
397	Gandia	7.3	39	35	Trammel net	Drowned and was resuscitated	08/05/18	Convalescent
399	Cullera	5.7	40	35	Trammel net	Healthy	06/06/18	Healthy
402	Burriana	5.7	36	33	Trawl/ bottom fishing	Healthy	29/05/18	Healthy
403	El Perello	7.24	38	35	Unknown (found floating at surface)	Healthy	11/06/18	Healthy
404	Almenara	3.24	30	28	Unknown (found floating at surface)	Wounded neck	13/06/18	Wounded neck
405	Peniscola	34.24	64	59	Trawl/ bottom fishing	Very mild GE	26/06/18	Healthy

Continued.

Appendix B (Chapter 3)

Table B1. Summary of tagged turtles including turtle identification number, entry to and release dates from the rehabilitation centre, bycatch origin, turtle weight (kg), cause of injury/disease (when known) and the turtle's state of health upon entry and on the date of tagging (following veterinary examination). Table ordered by turtle entry date. NB: gas emboli (GE) was categorised as mild, moderate, or severe; turtles that entered with GE were considered 'convalescent' when tagged within a couple of days of admission as they were only released into holding tanks following hyperbaric chamber treatment and once there was no sign of GE in the blood.

Turtle ID	Entry	Release	Origin	Weight (kg)	Cause of injury/ disease	State of health upon entry	Tagging date	State of health when tagged
T344	26/09/17	18/12/17	Vinaroz	12.1	Trammel net	Healthy	29/11/17	Healthy
T345	02/11/17	20/12/17	Vinaroz	17.1	Trammel net	Healthy	29/11/17	Healthy
T350	28/11/17	27/12/17	Peniscola	15	Trawl/ bottom fishing	Moderate GE	29/11/17	Convalescent
T359	02/01/18	04/03/18	Benicarlo	20.8	Trawl/ bottom fishing	Moderate GE	03/01/18	Convalescent
T362	16/01/18	06/03/18	Cullera	13	Trawl/ bottom fishing	Moderate GE	09/02/18	Healthy
T383	14/03/18	14/04/18	Cullera	11.6	Trawl/ bottom fishing	Moderate GE	15/03/18	Convalescent
T384	15/03/18	06/04/18	El Saler	15.2	Trawl/ bottom fishing	Mild GE	16/03/18	Convalescent
T385	18/03/18	20/07/18	Valencia	8.6	Trawl/ bottom fishing	Healthy	15/06/18	Healthy
T393	28/03/18	04/05/18	El Saler	28.71	Trawl/ bottom fishing	Moderate GE	18/04/18	Convalescent
T396	28/03/18	05/07/18	Vinaroz	22	Trawl/ bottom fishing	Healthy	08/05/18	Healthy
T397	05/04/18	03/06/18	Gandia	7.3	Trammel net	Drowned and was resuscitated	08/05/18	Healthy
T399	06/04/18	08/06/18	Cullera	5.7	Trammel net	Healthy	06/06/18	Healthy
T402	16/04/18	09/06/18	Burriana	5.7	Trawl/ bottom fishing	Healthy	29/05/18	Healthy
T403	06/05/18	29/06/18	El Perello	7.24	Unknown (found floating at surface)	Healthy	11/06/18	Healthy
T404	07/05/18	06/07/18	Almenara	3.24	Unknown (found floating at surface)	Wounded neck	22/06/18	Healthy
T405	01/06/18	12/07/18	Peniscola	34.24	Trawl/ bottom fishing	Very mild GE	26/06/18	Healthy

T443	23/01/19	14/03/19	Vinaroz	10.77	Trawl/ bottom fishing	Severe GE	25/01/19	Convalescent
T234	30/01/19	TBC	Burriana	85.5	Trawl/ bottom fishing	Mild GE and fishing hook ingestion	13/03/19	Healthy
T449	05/02/19	19/03/19	Peniscola	10.41	Trawl/ bottom fishing	Moderate GE	06/02/19	Convalescent
T452	13/02/19	09/03/19	Vinaroz	3.95	Trawl/ bottom fishing	Healthy	01/03/19	Healthy
T458	25/02/19	Died 29/03/19	Peniscola	41.28	Trawl/ bottom fishing	Severe GE	01/03/19	Convalescent (died of septicaemia and intestinal issues of unknown cause)
T459	25/02/19	26/04/19	Burriana	12.15	Trawl/ bottom fishing	Healthy	05/03/19	Healthy
T462	04/03/19	14/04/19	Benicarlo	13.47	Trawl/ bottom fishing	Mild GE	05/03/19	Convalescent
T463	04/03/19	28/06/19	Vinaroz	7.5	Trawl/ bottom fishing	Healthy	05/03/19	Healthy
T476	22/03/19	16/06/19	Vinaroz	15	Trawl/ bottom fishing	Healthy	04/06/19	Healthy
T477	25/03/19	08/06/19	Gandia	9.9	Trammel net	Superficial injury to the cloaca	04/06/19	Healthy
T481	05/04/19	07/06/19	Cullera	25.18	Trawl/ bottom fishing	Healthy	04/06/19	Healthy
T482	11/04/19	03/07/19	Peniscola	30	Trawl/ bottom fishing	Moderate GE	11/06/19	Healthy
T484	26/04/19	02/07/19	Peniscola	13.53	Trawl/ bottom fishing	Mild GE	11/06/19	Healthy

Continued.

**TBC; To be confirmed.*

Appendix C (Chapter 3)

Exponential decay curves drawn with values extracted from 24-hour VeDBA frequency distributions for healthy turtles and convalescent turtles (for more information regarding turtles see Chapter 3, Table 1). The exponential decay curves were drawn in RStudio using a self-starting function ‘SSasymp’, which estimated its own start parameters.

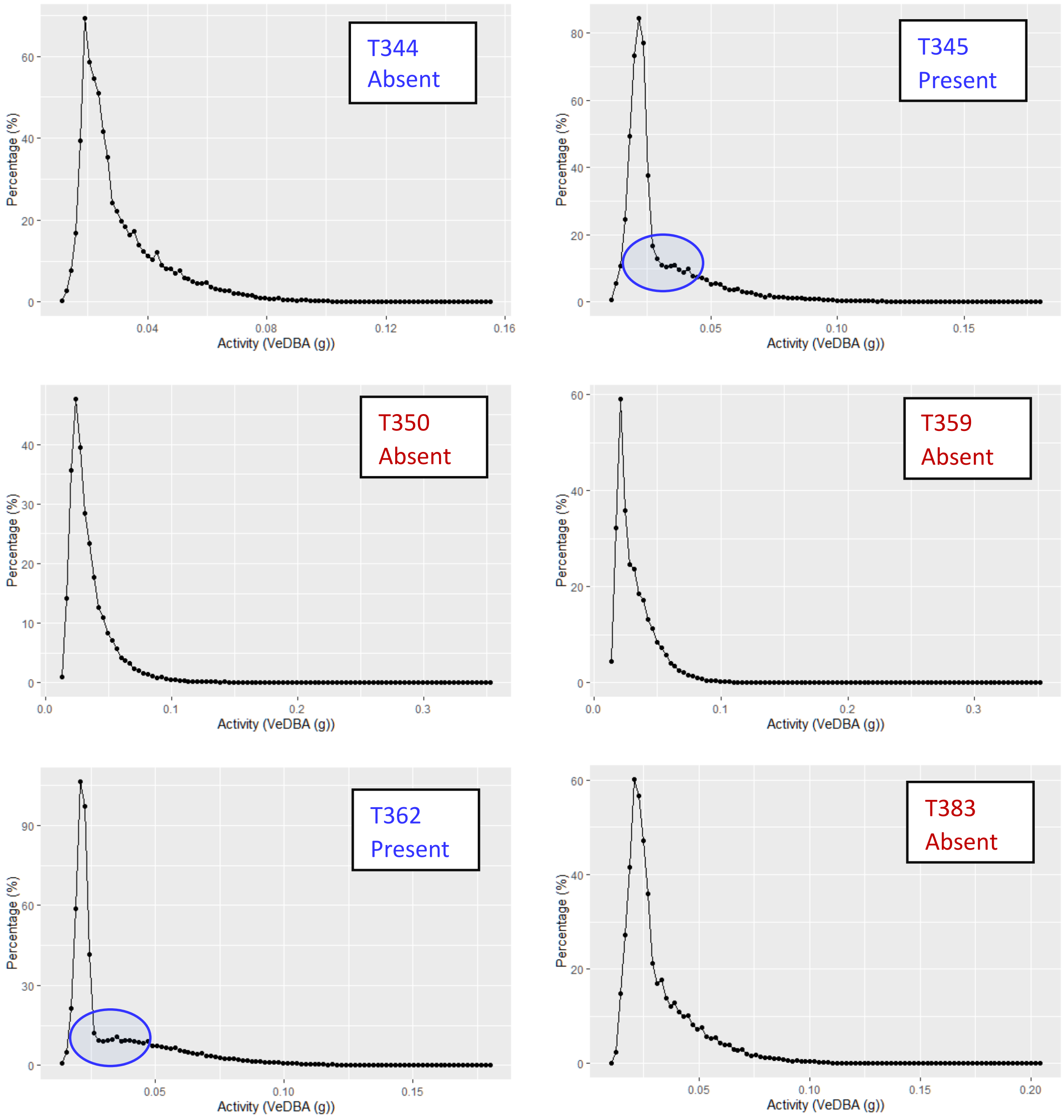
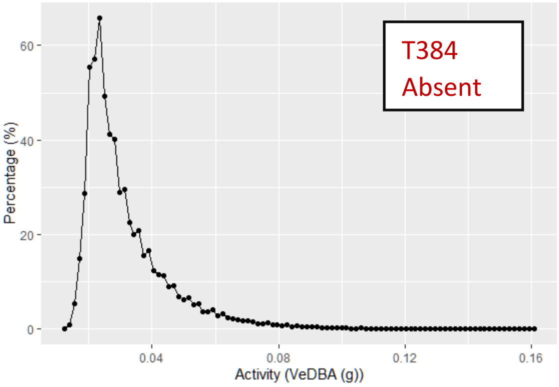
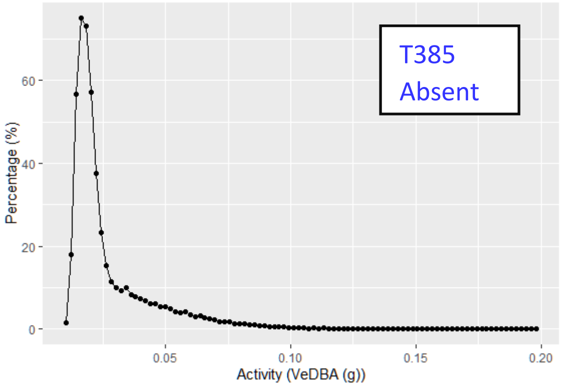
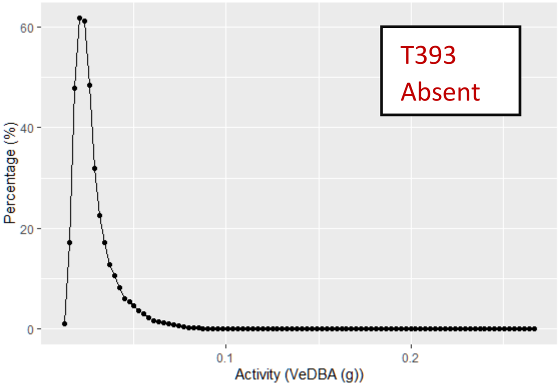
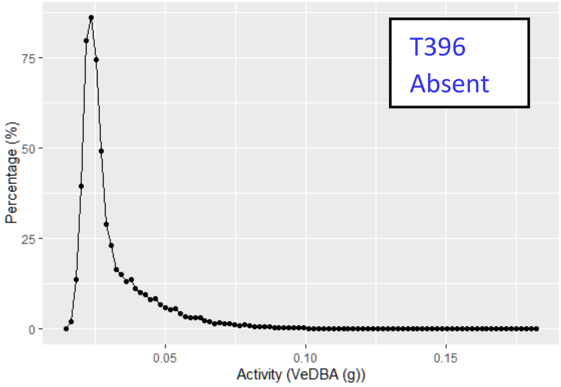


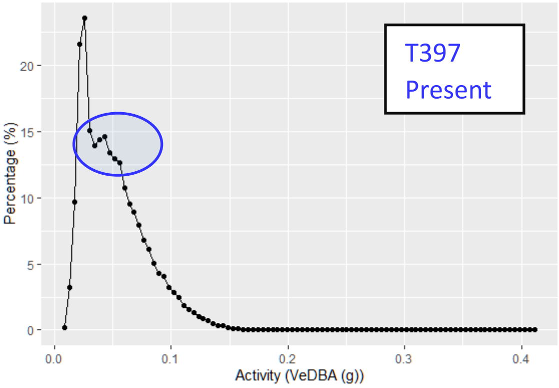
Figure C1. [Continued over 4 pages]. Exponential decay curves drawn for healthy turtles (blue) and GE recovering turtles (red) and ordered according to turtle entry date (Chapter 3, Table 1). Healthy and convalescent turtle 24-hour VeDBA frequency distributions did not always differ in the predicted manner, i.e., that inflection points would be visible in all healthy turtle distributions. Clear inflection points (circled in blue) were present in the majority of healthy turtles, being absent in only 6/20 healthy individuals’; they were also absent in all GE animals.

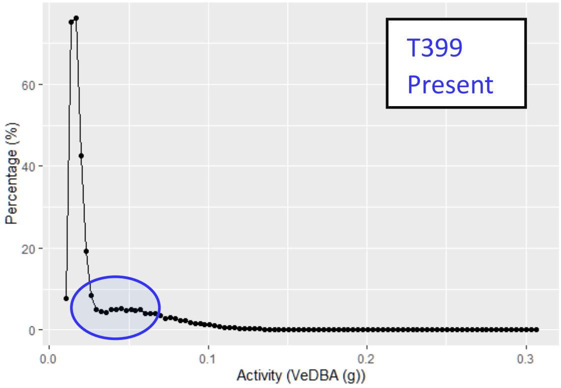

T384
Absent
Percentage (%)
0
20
40
60
0.04
0.08
0.12
0.16
Activity (VeDBA (g))

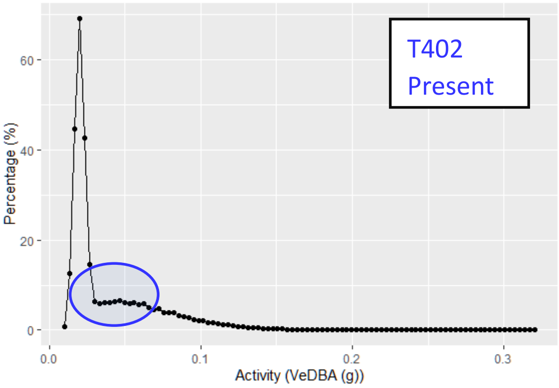

T385
Absent
Percentage (%)
0
20
40
60
0.05
0.10
0.15
0.20
Activity (VeDBA (g))

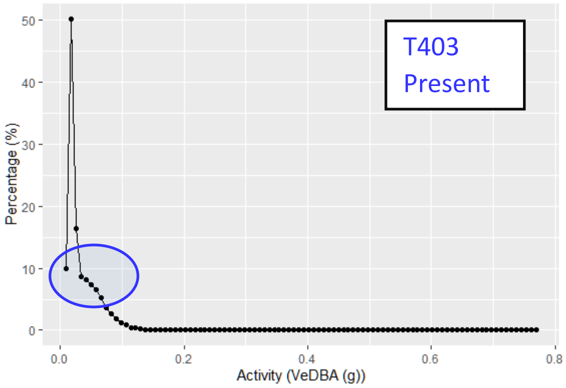

T393
Absent
Percentage (%)
0
20
40
60
0.1
0.2
Activity (VeDBA (g))


T396
Absent
Percentage (%)
0
25
50
75
0.05
0.10
0.15
Activity (VeDBA (g))

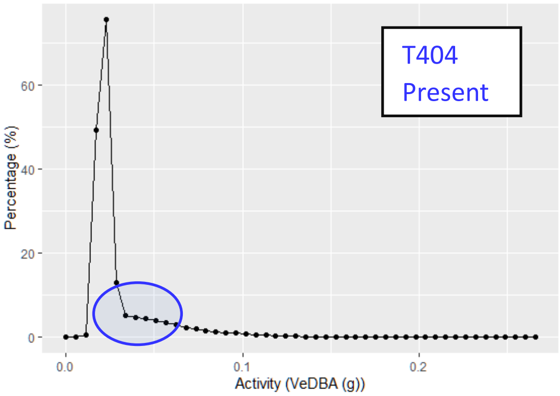

T397
Present
Percentage (%)
0
5
10
15
20
0.0
0.1
0.2
0.3
0.4
Activity (VeDBA (g))

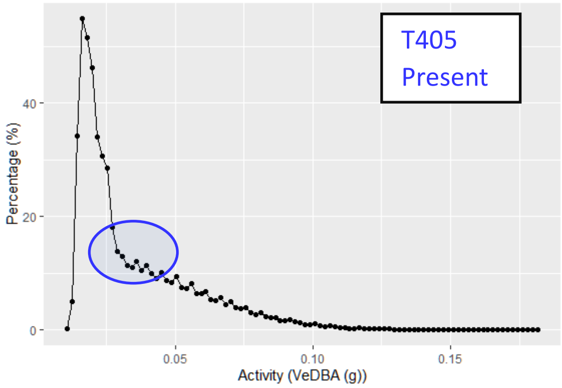

T399
Present
Percentage (%)
0
20
40
60
0.0
0.1
0.2
0.3
Activity (VeDBA (g))

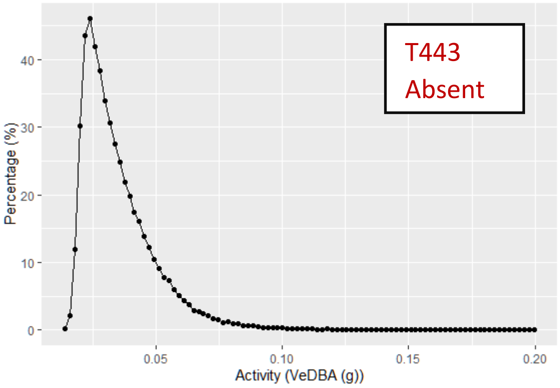

T402
Present
Percentage (%)
0
20
40
60
0.0
0.1
0.2
0.3
Activity (VeDBA (g))

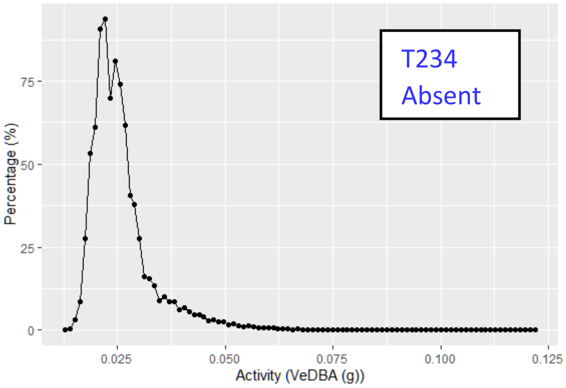

T403
Present
Percentage (%)
0
10
20
30
40
50
0.0
0.2
0.4
0.6
0.8
Activity (VeDBA (g))

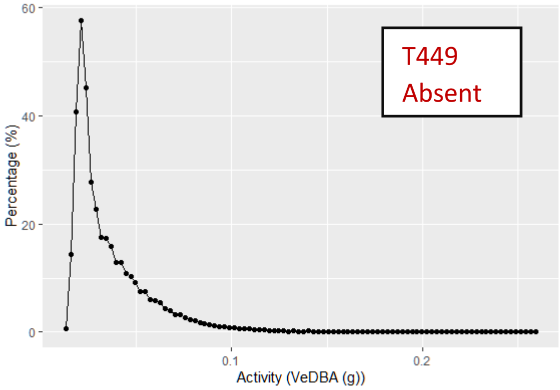
Appendix C (Chapter 3, *continued*)

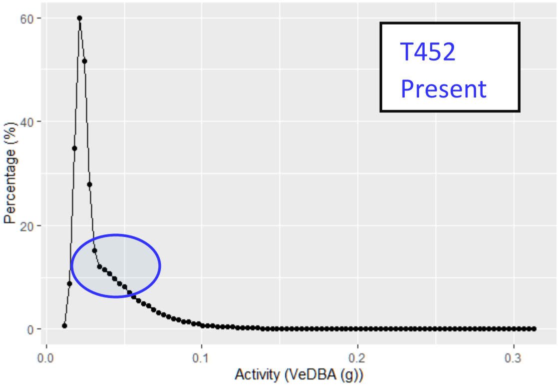


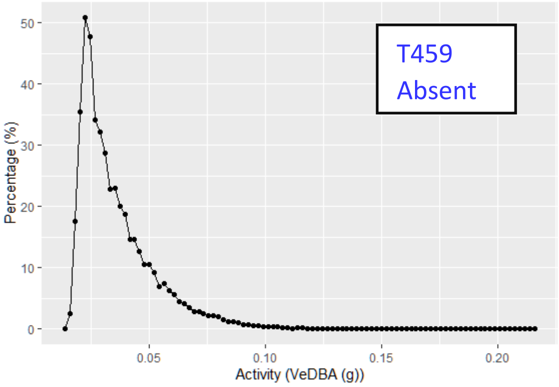


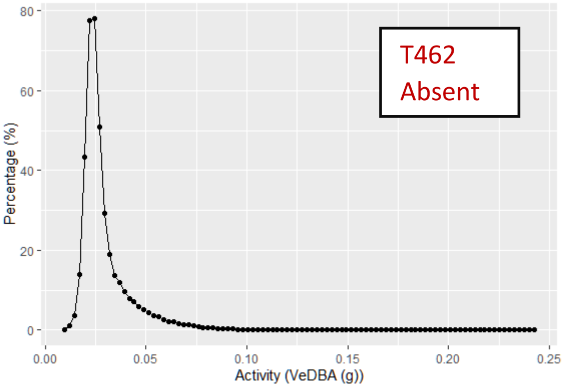




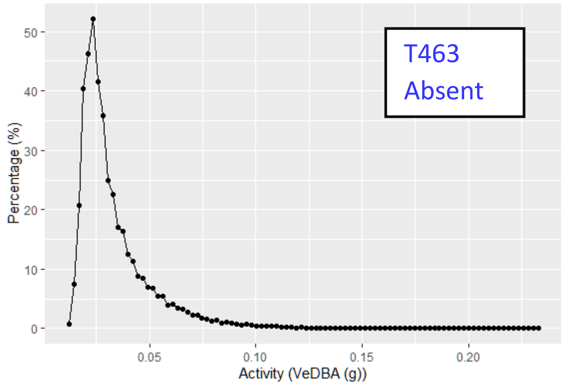


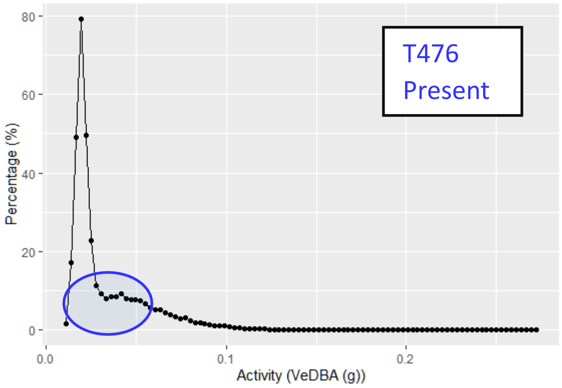


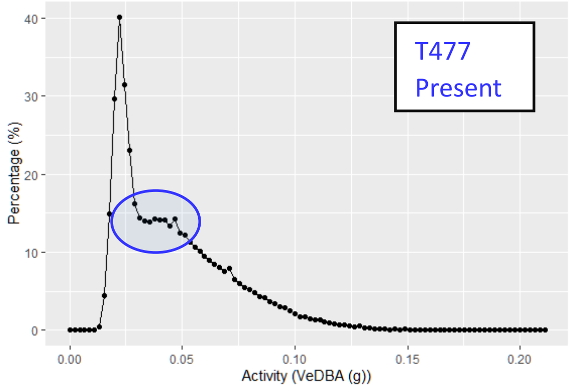


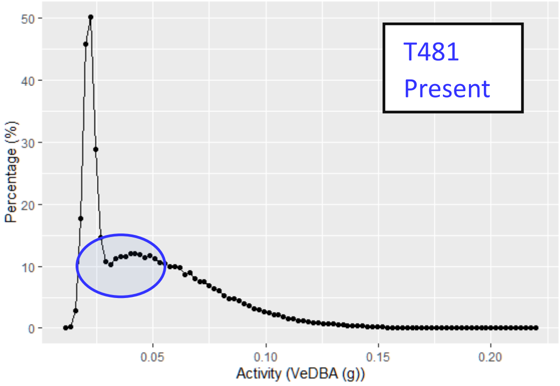


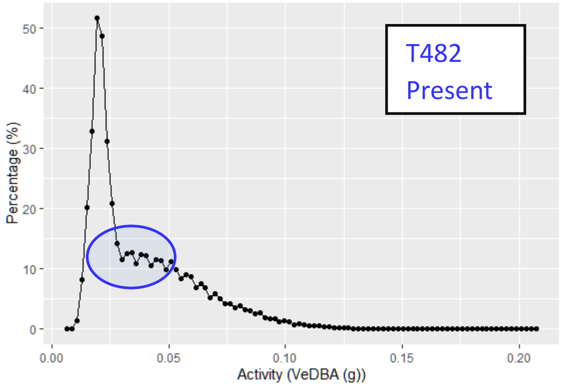
Appendix C (Chapter 3, *continued*)

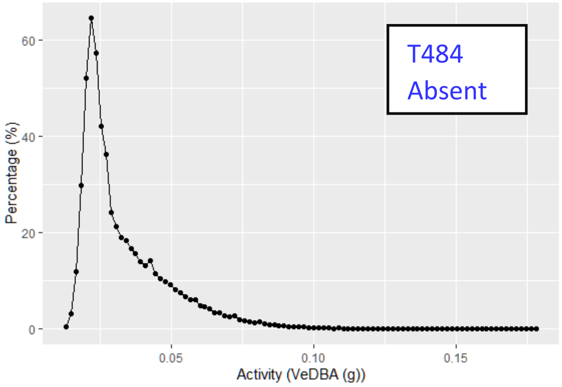












Appendix D (Chapter 3)

Similar set of graphs as presented in Chapter 3, Figure 9, but drawn with mean VeDBA instead of VeDBA variance.

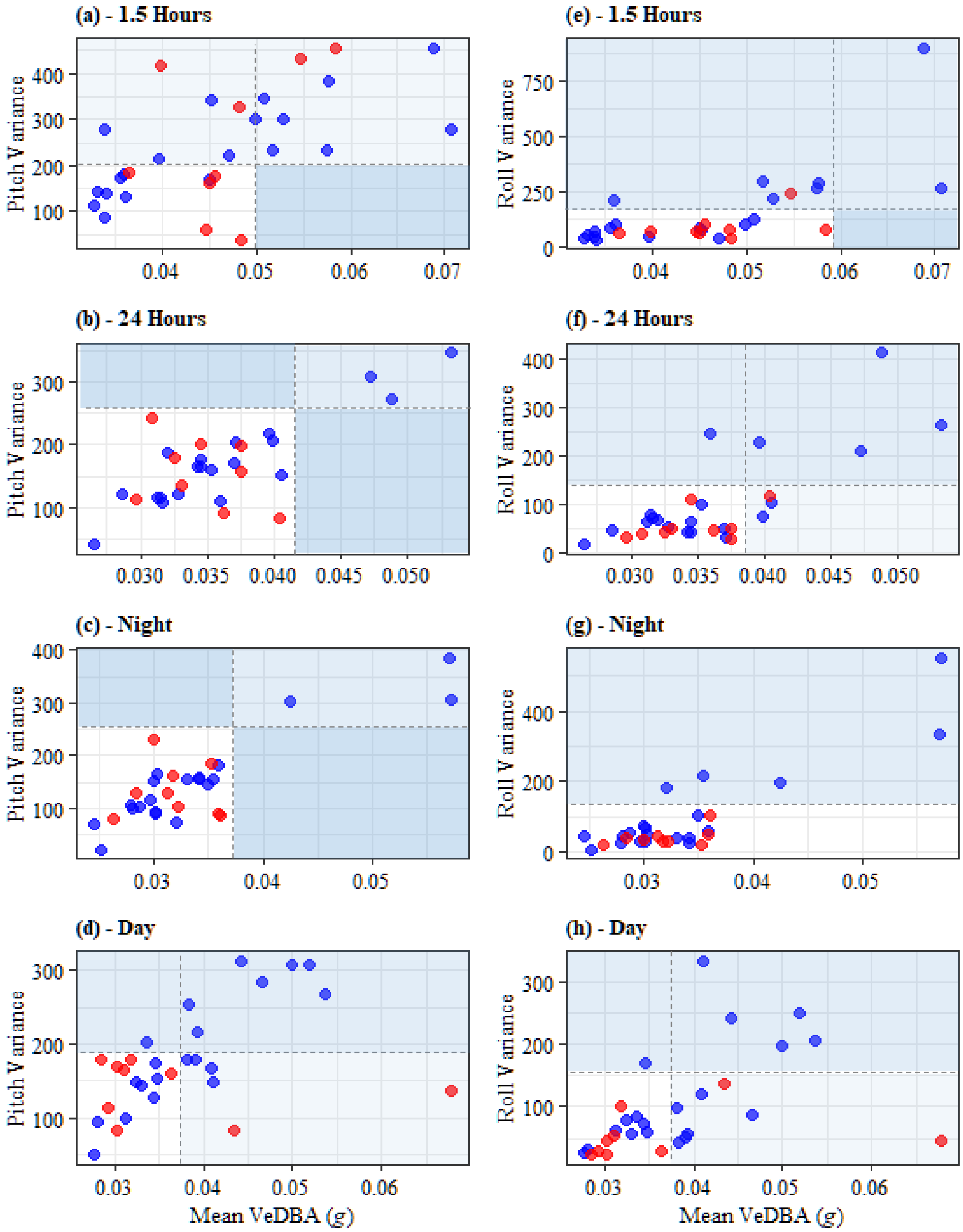


Figure D1. Mean VeDBA (g) per turtle against variance in pitch (a–d) and roll (e–h) for healthy turtles (in blue; n = 18) and convalescent turtles (in red; n = 9). Variance in pitch and roll was calculated over periods of (a, e) 1.5 hours, (b, f) 24 hours, (c, g) at night (20:00–8:00) and (d, h) during the day (8:00–20:00). Values from convalescent turtles generally fell within the healthy turtle range; however, all points in the top right-hand corner of graphs with a higher variance were exclusively from healthy turtles. The dotted lines defined areas where healthy and convalescent turtle values overlapped (not shaded), areas with a majority of healthy turtles (and only one or two convalescent turtles; light shading) areas exclusive to healthy turtles (medium shading) and areas with no turtles (darker shading).

Appendix E (Chapter 3)

Regressions showing the relationship between mean VeDBA and turn angle (Figures E1–8).

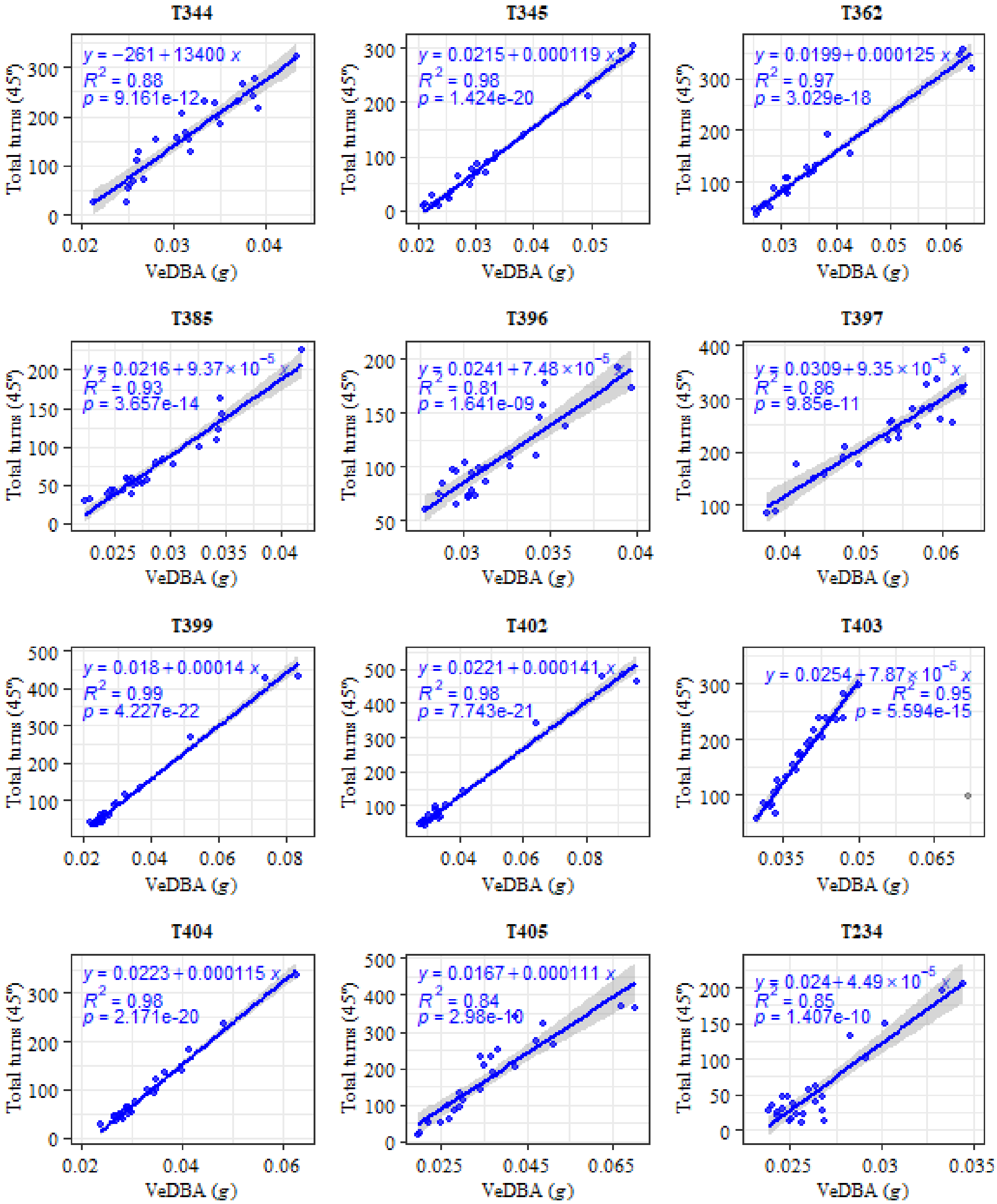


Figure E1. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 45° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (healthy = blue); 95% confidence intervals were indicated by the grey shading either side of regression lines. An outlier, in T403's data (coloured grey), was removed from the points included in the regression.

Appendix E (Chapter 3, *continued*)

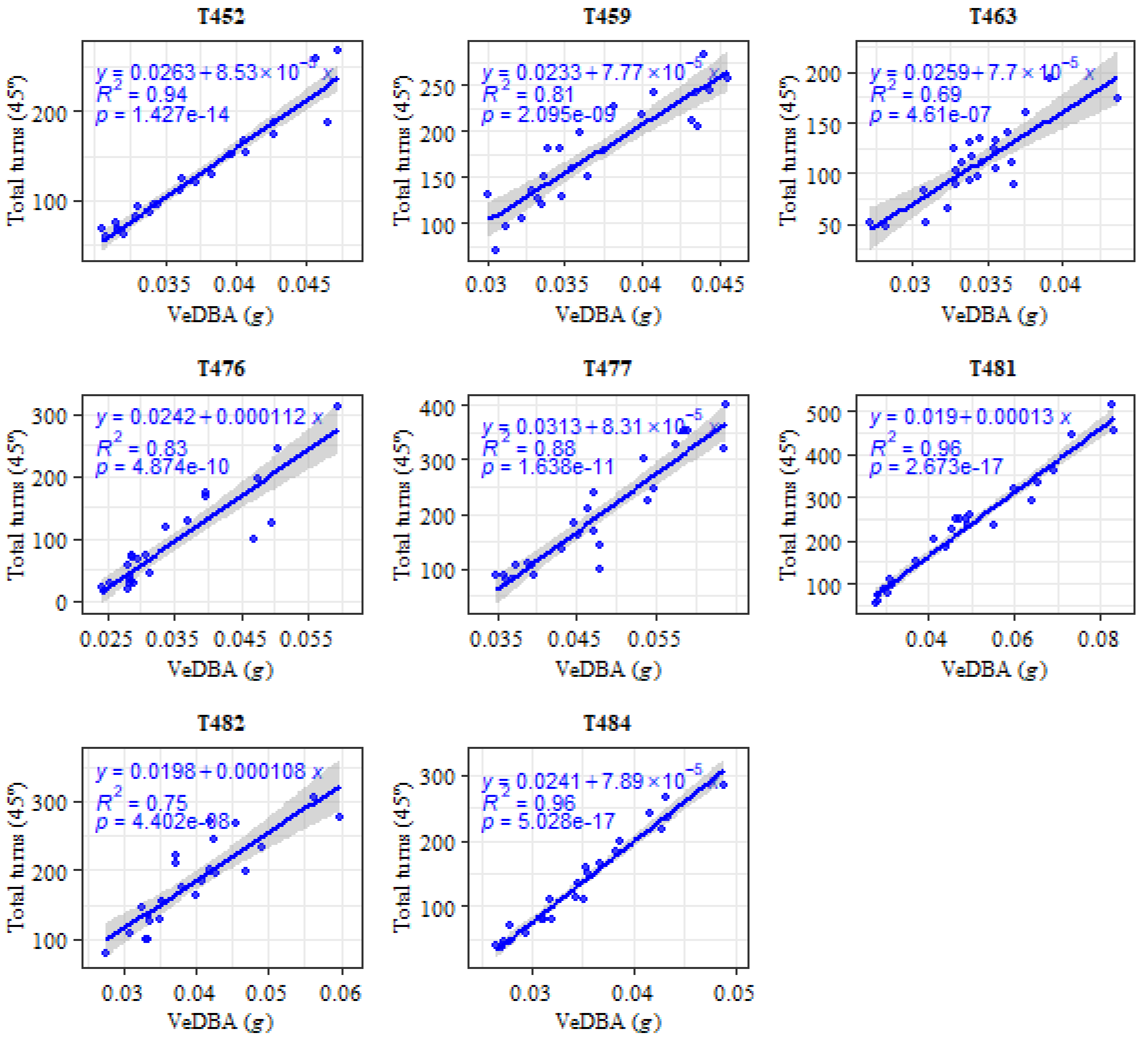


Figure E1. [Continued]. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 45° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (healthy = blue); 95% confidence intervals were indicated by the grey shading either side of regression lines.

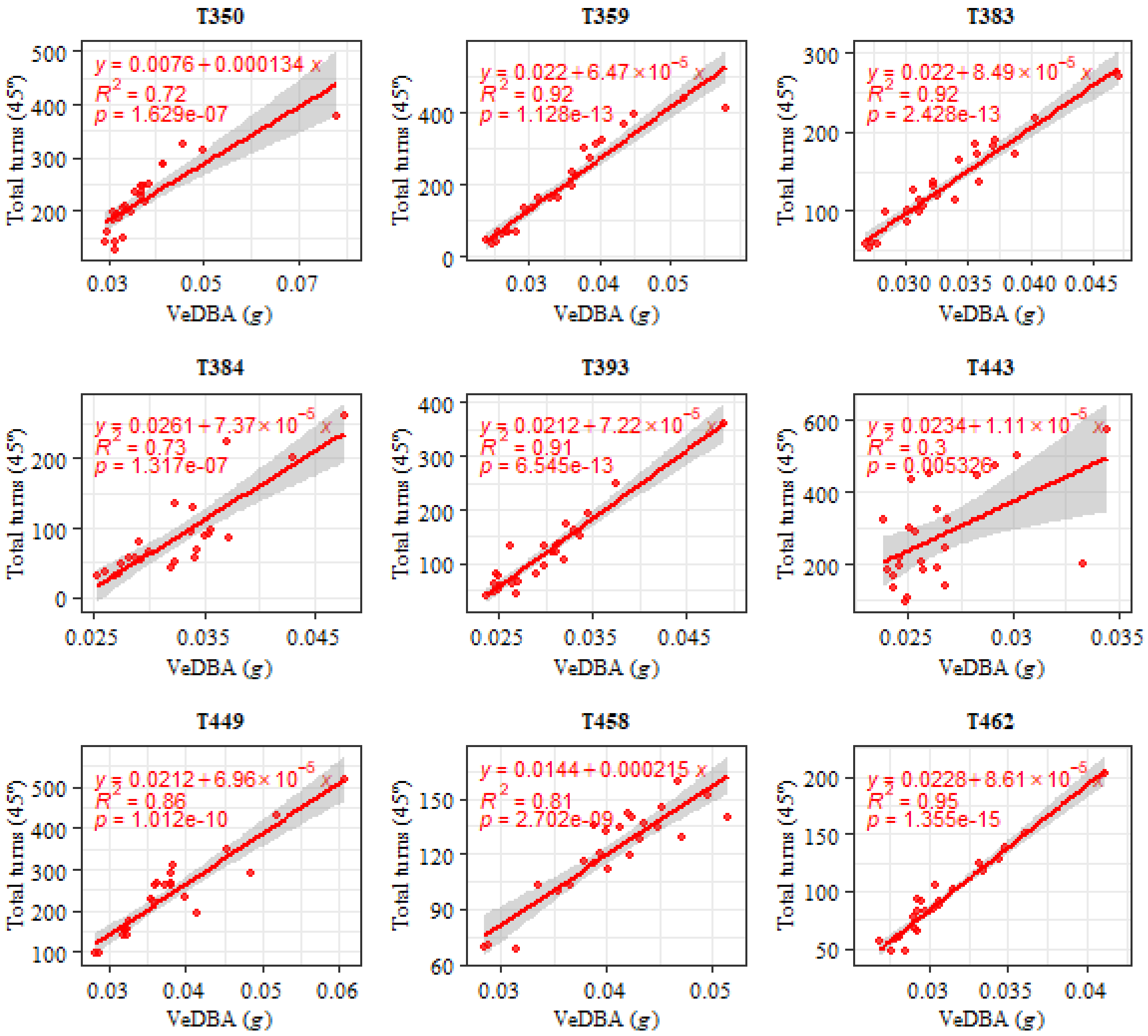


Figure E2. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 45° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (convalescent = red); 95% confidence intervals were indicated by the grey shading either side of regression lines.

Appendix E (Chapter 3, *continued*)

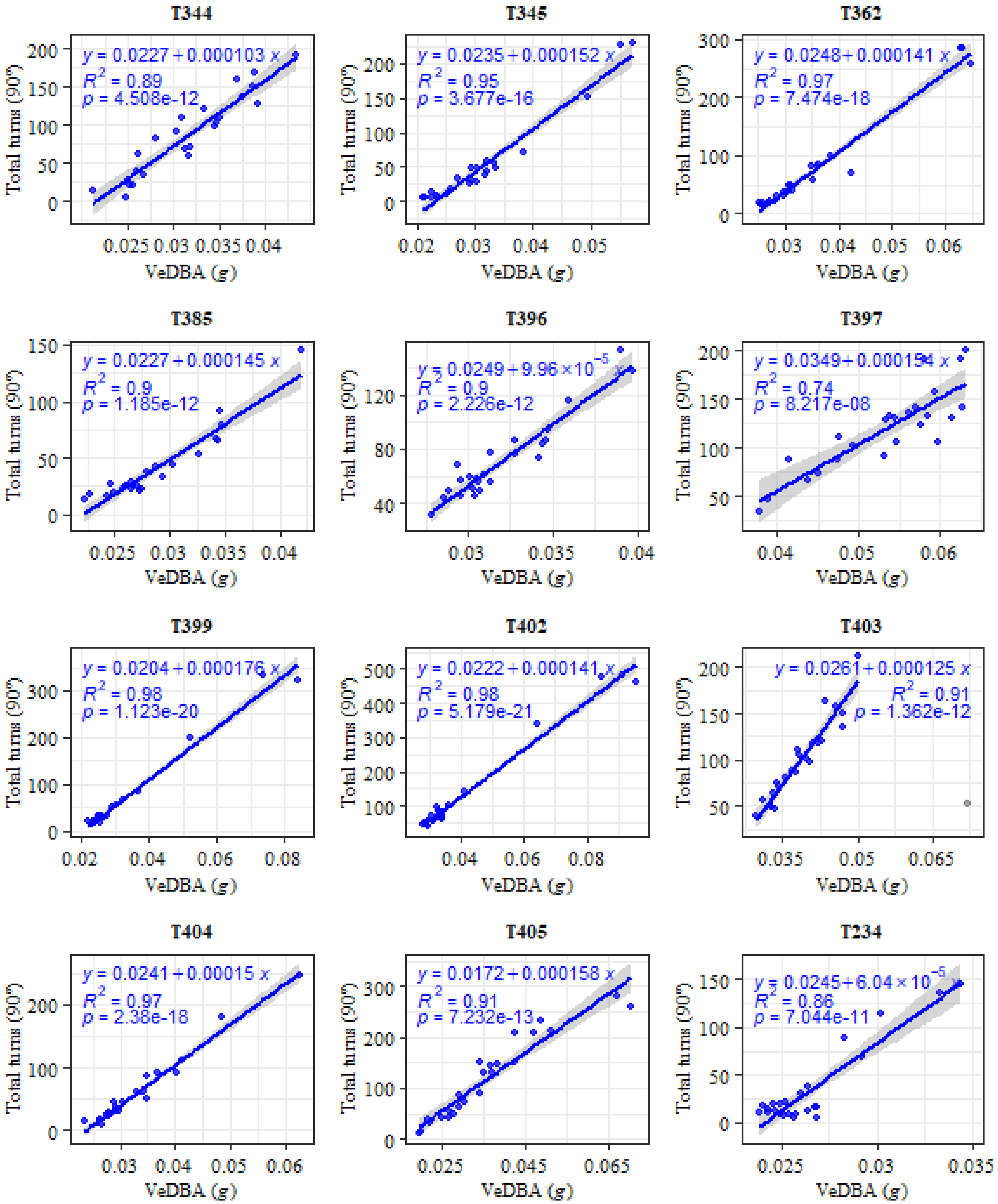


Figure E3. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 90° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (healthy = blue); 95% confidence intervals were indicated by the grey shading either side of regression lines. An outlier, in T403's data (coloured grey), was removed from the points included in the regression.

Appendix E (Chapter 3, *continued*)

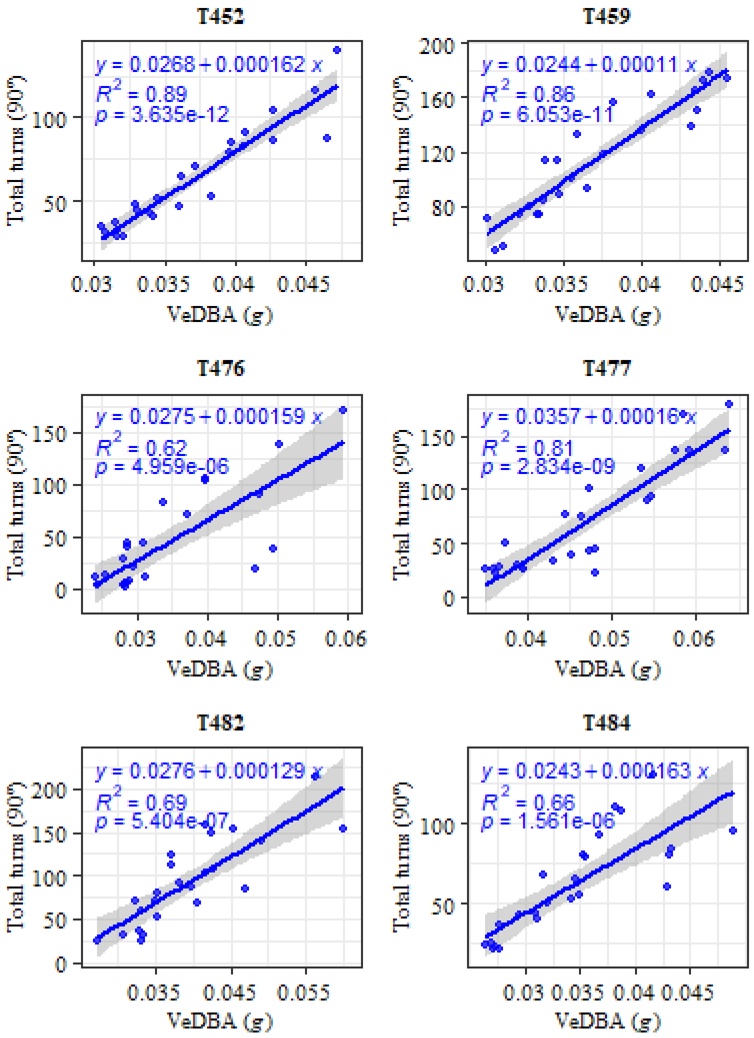


Figure E3. [Continued]. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 90° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (healthy = blue); 95% confidence intervals were indicated by the grey shading either side of regression lines.

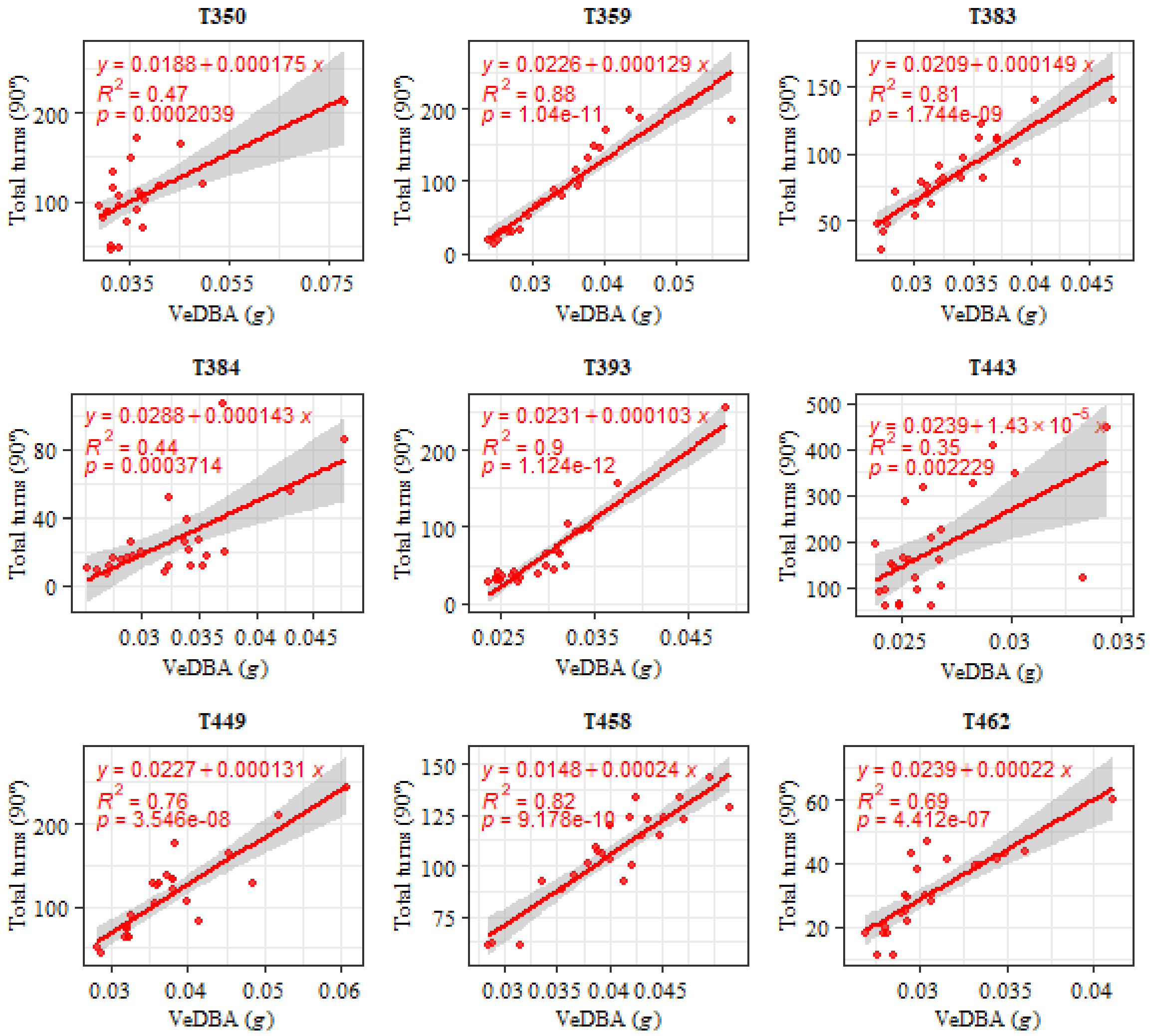


Figure E4. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 90° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (convalescent = red); 95% confidence intervals were indicated by the grey shading either side of regression lines.

Appendix E (Chapter 3, *continued*)

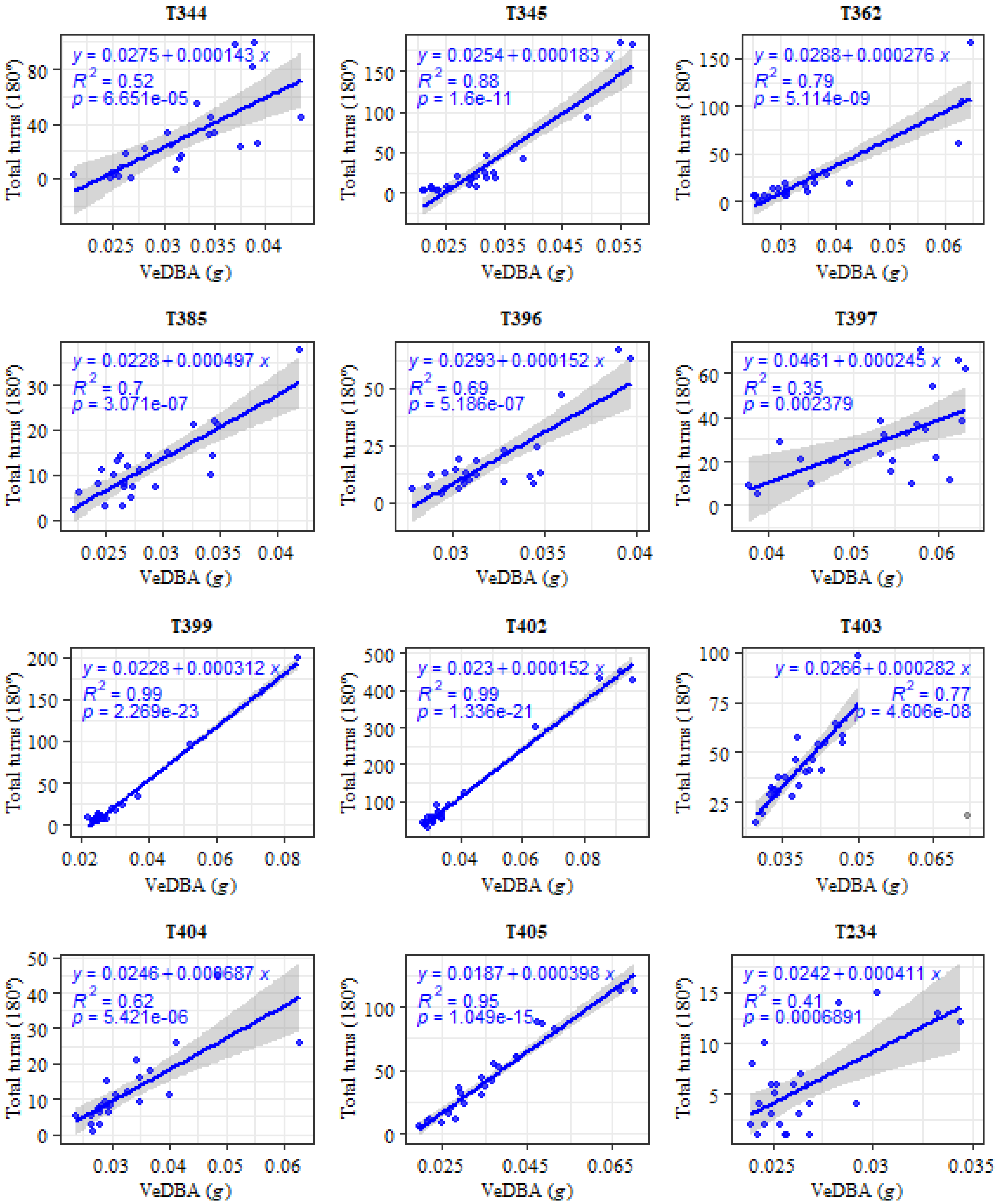


Figure E5. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 180° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (healthy = blue); 95% confidence intervals were indicated by the grey shading either side of regression lines. An outlier, in T403's data (coloured grey), was removed from the points included in the regression.

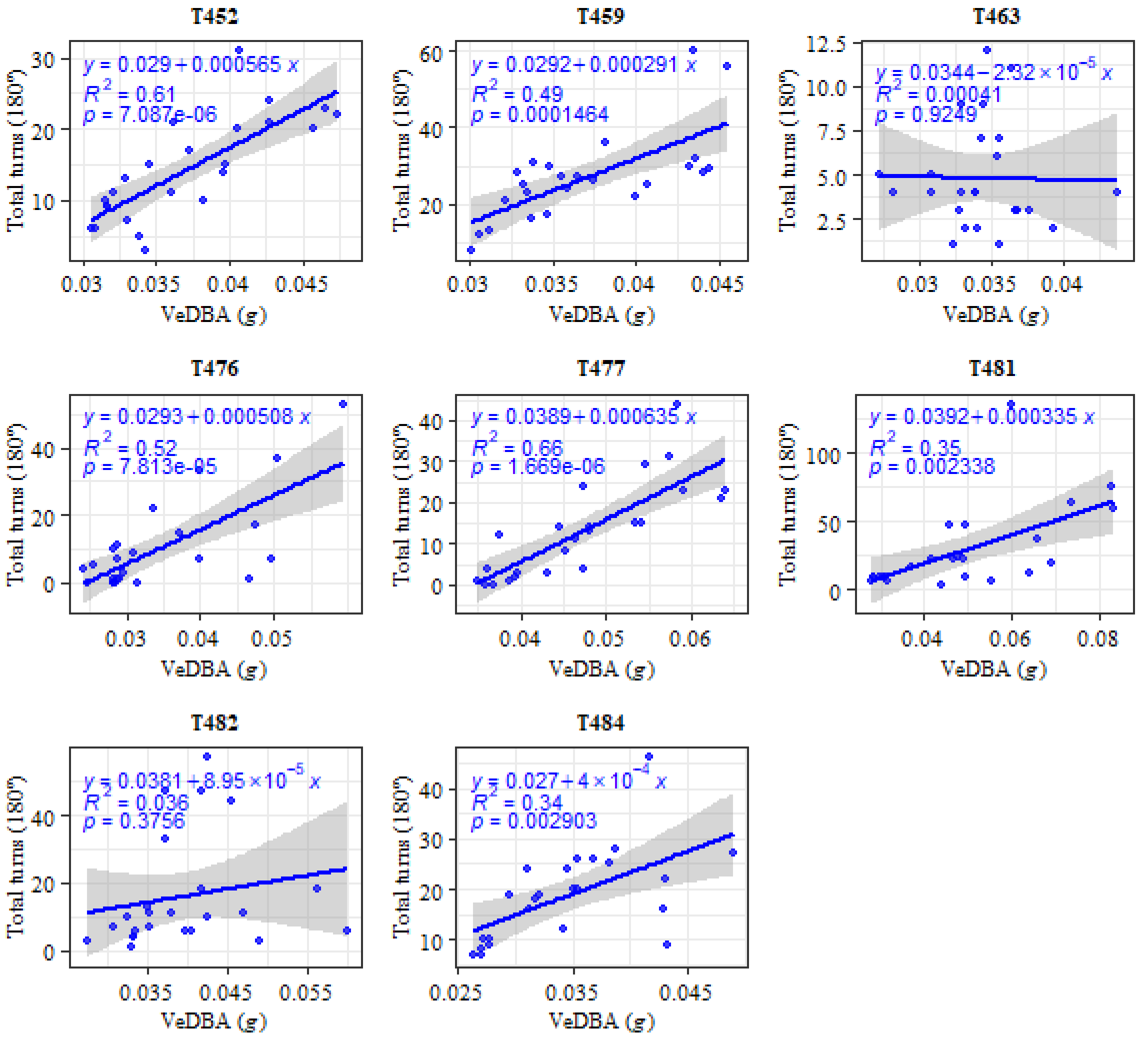


Figure E5. [Continued]. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 180° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (healthy = blue); 95% confidence intervals were indicated by the grey shading either side of regression lines.

Appendix E (Chapter 3, *continued*)

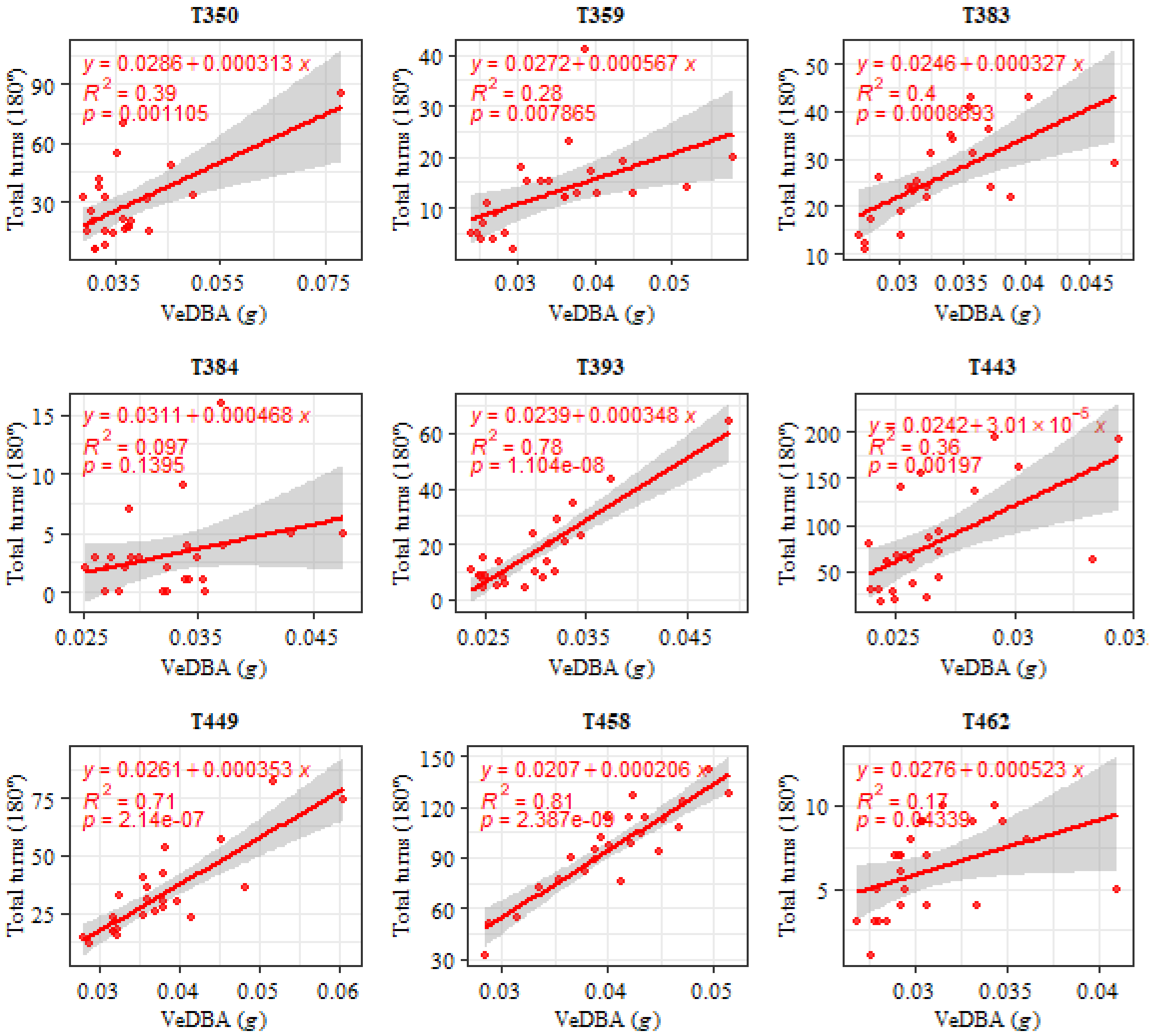


Figure E6. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 180° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (convalescent = red); 95% confidence intervals were indicated by the grey shading either side of regression lines.

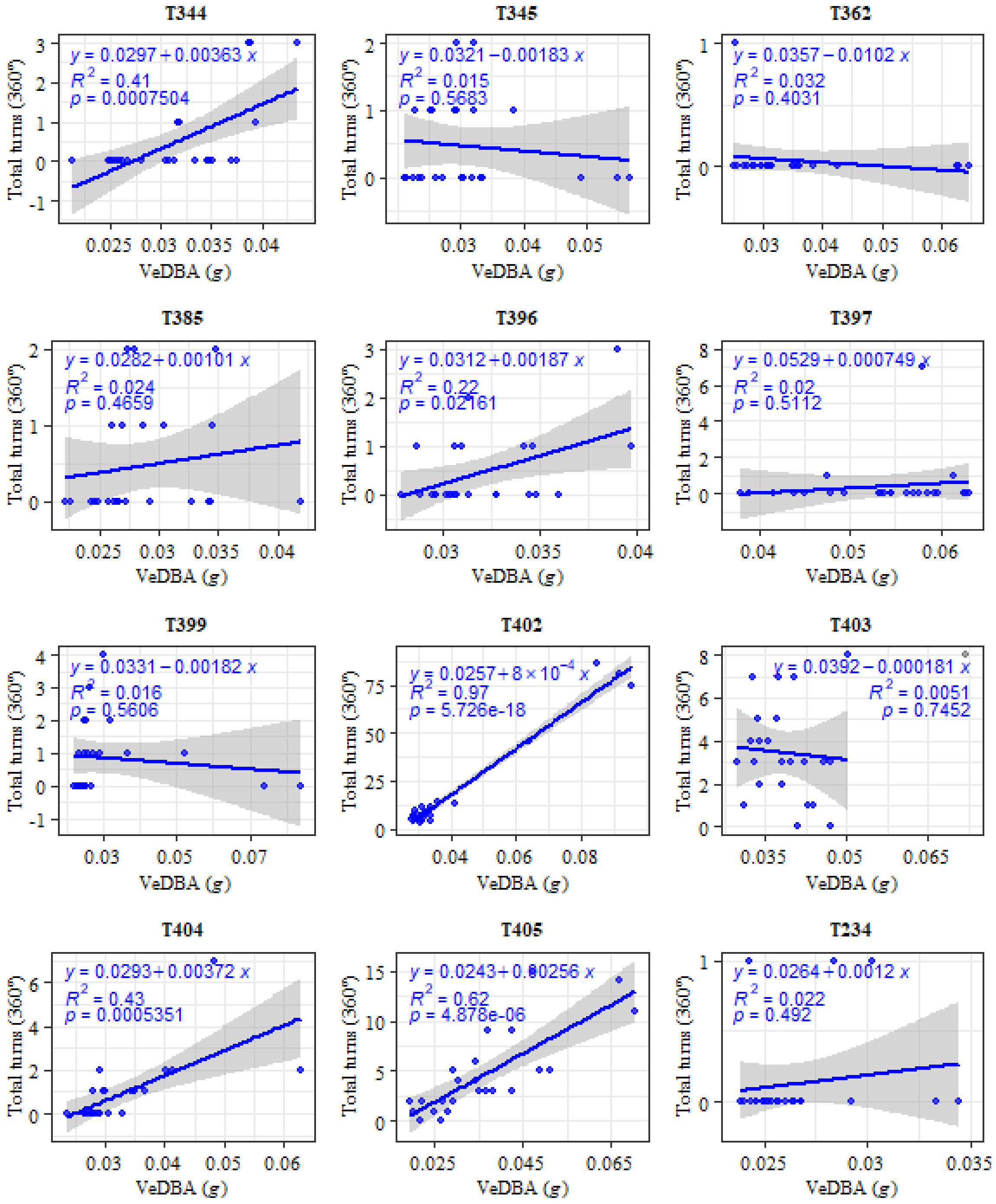


Figure E7. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 360° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (healthy = blue); 95% confidence intervals were indicated by the grey shading either side of regression lines. An outlier, in T403's data (coloured grey), was removed from the points included in the regression.

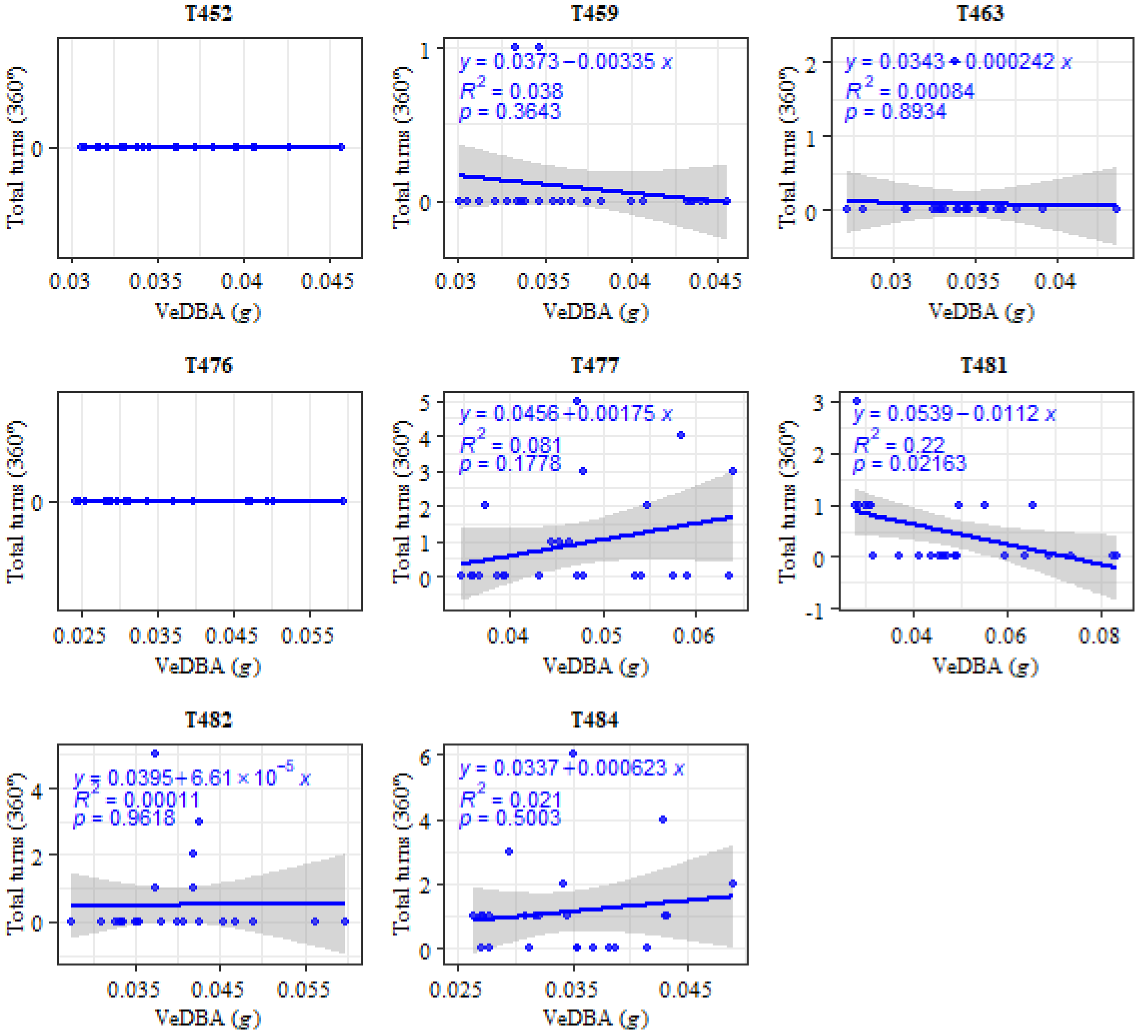


Figure E7. [Continued]. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 360° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (healthy = blue); 95% confidence intervals were indicated by the grey shading either side of regression lines.

Appendix E (Chapter 3, *continued*)

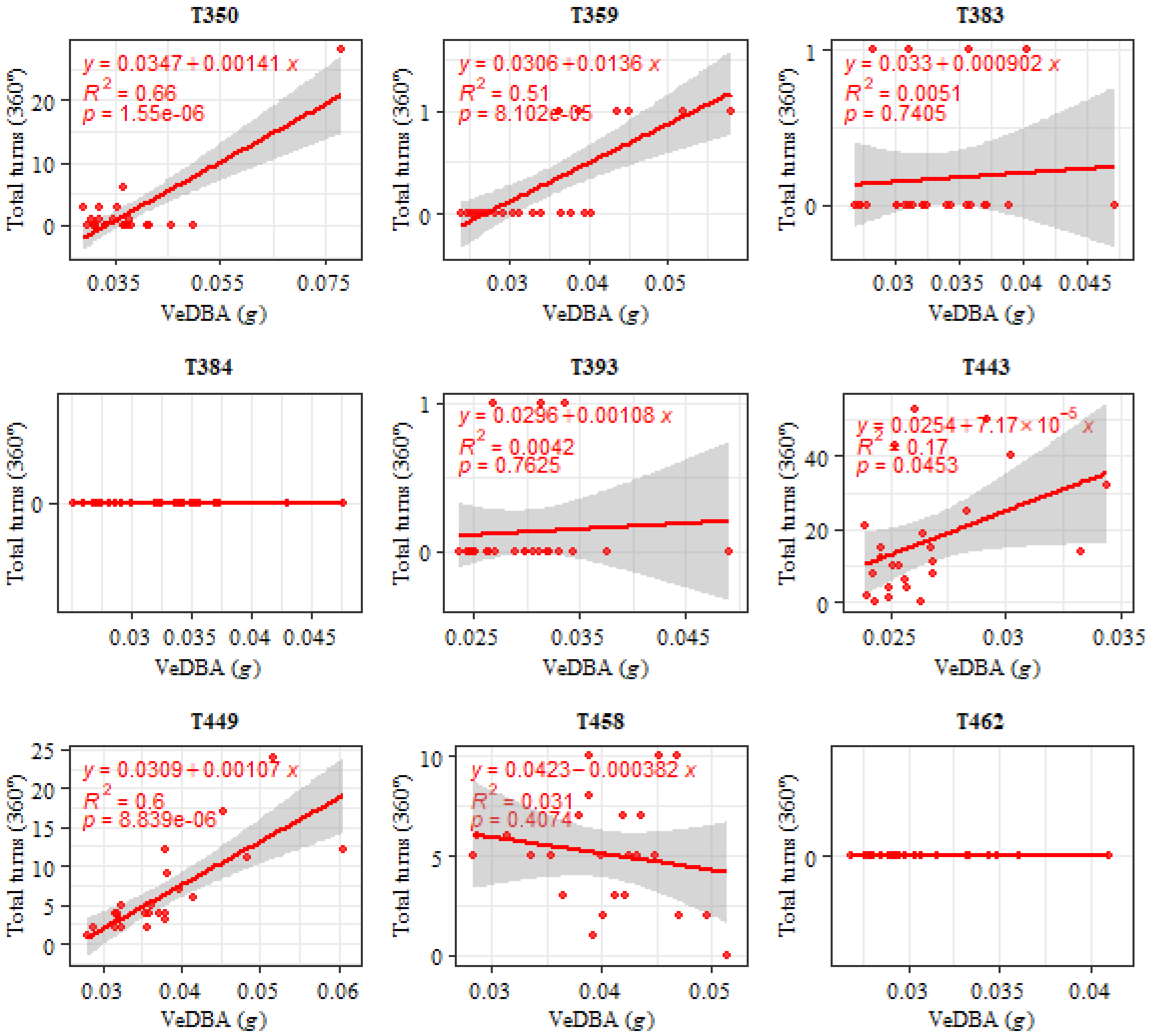


Figure E8. Relationship between mean VeDBA (g) and the total number of turns per hour that surpassed a threshold of 360° during a 24-hour tagging window (that began after a 1-hour acclimatization period). Each data point represented one hour of data, resulting in 24 data points per turtle; graph titles indicate which turtle the data belonged to (cf. Chapter 3, Table 1). Points and regression lines were colored according to turtle condition (convalescent = red); 95% confidence intervals were indicated by the grey shading either side of regression lines.

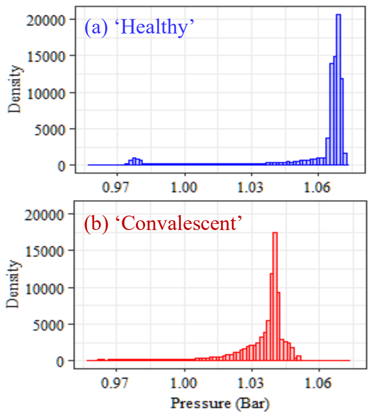
Appendix F (Chapter 3)

Identification Key: Healthy *vs* Convalescent Turtles

This identification key incorporates movement metrics defined in Chapter 3 and has been created to show how such metrics could aid in the assessment of rehabilitating turtle health, specifically that of turtles recovering from gas emboli (convalescent). In theory, vets would go through the key, ticking the healthy, 'H' or convalescent, 'C' turtle box according to what best resembled their turtle. The number of each would then be tallied to see if the turtle was more likely to be healthy or convalescent. To make a key like this practical for veterinary use, a program that could read tag data and assess movement metrics automatically would be necessary.

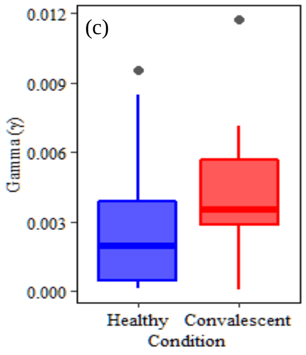
1. Over a 24-hour period, the pressure profile has:

- ☐ *(H) A small hump at low pressure and a large peak at high pressure resulting from momentarily surfacing to breathe and then resting on the tank floor respectively (see Fig. (a) for a 'healthy' turtle example).*
- ☐ *(C) A wider base and solitary peak indicating time spent at varying depths (see Fig. (b) for a 'convalescent' turtle example).*



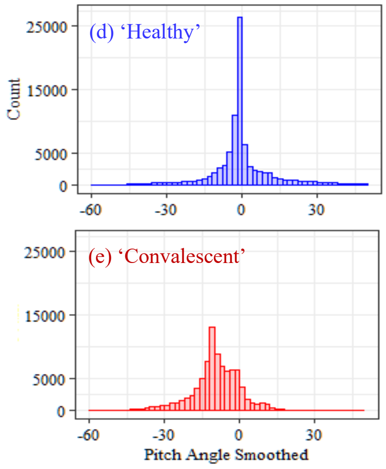
2. Fig. (c) Bent-cable model transition zone, i.e., 'gamma' results; models fit to 24-hour VeDBA distributions, using only data that fell in between the upper (90%) and lower (10%) decile. If the 'gamma' value is below 0.003 tick 'H', if above, tick 'C'.

- ☐ *(H) Gamma < 0.003*
- ☐ *(C) Gamma > 0.003*



3. Over a 24-hour period, pitch angles are:

- ☐ *(H) Fairly evenly distributed either side of 0° with a prominent central peak indicating time spent on the tank floor i.e., the horizontal plane (see Fig. (d) for a 'healthy' turtle example).*
- ☐ *(C) More heavily distributed towards the negative; values are more evenly spread over a wider range of angles resulting in a less prominent peak (see Fig. (e) for a 'convalescent' turtle example).*

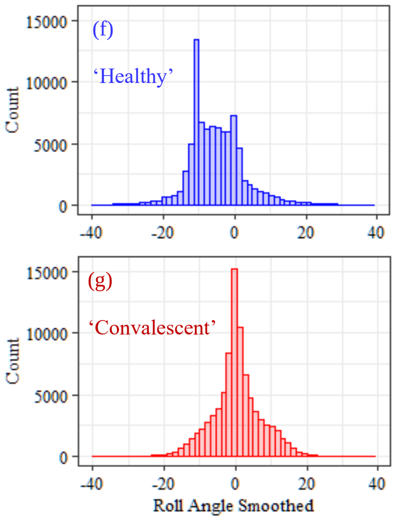


Identification Key: Healthy *vs* Convalescent Turtles

4. Over a 24-hour period, roll angles:

☐ *(H) Rise in a tower shape and may have two peaks indicating time spent swimming on the left and/or right side, one side may be dominant (see Fig. (f) for a 'healthy' turtle example).*

☐ *(C) Rise in a central peak with ends that taper towards the positive and negative extremes, indicating less time spent swimming on either the left or right side and perhaps a tendency to self-right (see Fig. (g) for a 'convalescent' turtle example).*



5. Variance in VeDBA and pitch during the day is greater than 0.00024 and 200, respectively. If true tick 'H', if not tick 'C'.

☐ *(H) VeDBA variance > 0.00024 + roll variance > 200*
☐ *(C) VeDBA variance < 0.00024 + roll variance < 200*

6. Variance in VeDBA and roll at night is greater than 0.00024 and 50, respectively. If true tick 'H', if not tick 'C'.

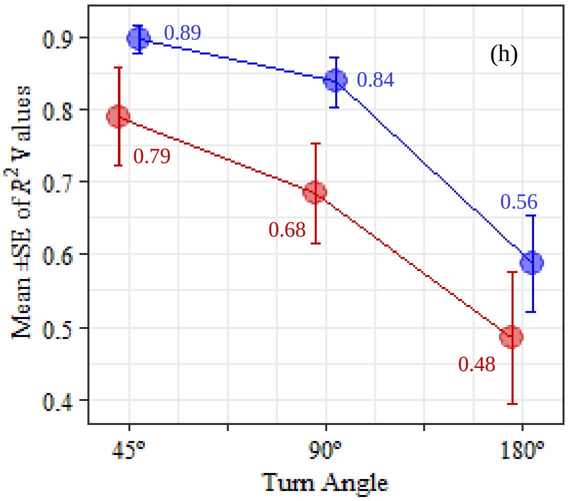
☐ *(H) VeDBA variance > 0.00024 + roll variance > 50*
☐ *(C) VeDBA variance < 0.00024 + roll variance < 50*

7. Variance in VeDBA during the day is greater than 0.00021 whilst variance in roll at night is greater than 140. If true tick 'H', if not tick 'C'.

☐ *(H) VeDBA variance > 0.00021 + roll variance > 140*
☐ *(C) VeDBA variance < 0.00021 + roll variance < 140*

8. Fig. (h) Mean ±SE of R² values obtained from linear regressions of mean VeDBA per hour against the total number of turns per hour reaching angles of: 45°, 90° and 180° over a 24-hour period. Healthy turtle R² values are shown in blue and convalescent turtles in red. For each turn angle find the R² value closest to your own; based on this, tick 'H' or 'C' as appropriate.

☐ *(H) 45°* ☐ *(H) 90°* ☐ *(H) 180°*
☐ *(C) 45°* ☐ *(C) 90°* ☐ *(C) 180°*



Appendix G (Chapter 4)

Table G1. Summary of tagged turtles including turtle identification number, entry to and release dates from the rehabilitation centre, bycatch origin, turtle weight (kg), cause of injury/disease (when known), the turtle's state of health upon entry and the date of the turtle's first trial (also the first date of tagging). All animals were 'healthy' when tagged. State of health was deduced following veterinary examination; gas emboli (GE) was categorised according to methods described in García-Párraga et al. (2014) and Fahlman et al. (2017).

Turtle ID	Entry	Release	Origin	Weight (kg)	Cause of injury/ disease	State of health upon entry	Date of first trial
T348	21/11/2017	13/07/2018	Vinaroz	4.06	Trawl/ bottom fishing	Mild GE	28/06/2018
T385	18/03/2018	20/07/2018	Valencia	8.6	Trawl/ bottom fishing	Healthy	21/06/2018
T396	28/03/2018	05/07/2018	Vinaroz	22	Trawl/ bottom fishing	Healthy	28/06/2018
T397	05/04/2018	03/06/2018	Gandia	7.3	Trammel net	Drowned and resuscitated	30/05/2018
T399	06/04/2018	08/06/2018	Cullera	5.7	Trammel net	Healthy	30/05/2018
T402	16/04/2018	09/06/2018	Burriana	5.7	Trawl/ bottom fishing	Healthy	30/05/2018
T403	06/05/2018	29/06/2018	El Perello	7.24	Unknown (found floating at surface)	Healthy	11/06/2018
T404	07/05/2018	06/07/2018	Almenara	3.24	Unknown (found floating at surface)	Wounded neck	11/06/2018
T405	01/06/2018	12/07/2018	Peniscola	34.24	Trawl/ bottom fishing	Very mild GE	28/06/2018

Appendix H (Chapter 5)

Table H1. Summary information of all turtles tagged within a controlled environment; column headings from left to right detail the turtle identification number, date of entry, date of release from the rehabilitation centre, origin (i.e., bycatch location), turtle weight (kg), bycatch gear, state of health upon entry, date of tagging, tank size given as the available water volume (L) and the state of health when tagged. Upon arrival, a veterinary health assessment categorised animals as, 'healthy' (i.e. free of injury and disease) or with very mild to moderate gas emboli (GE) which was scored following methods detailed in García-Párraga et al. (2014) and Fahlman et al. (2017). All animals were healthy when tagged. If a turtle was tagged in an exhibit this is indicated after the tank size; turtles tagged in an outdoor exhibit with seals are indicated with an '' and turtles tagged in an indoor tank with deep sea shark species and other fish and 3D structures are indicated with an '**'. Rows with ' " ' indicate that a turtle was tagged twice, and the information is replicated in the row above. Turtle identification numbers are a running count of the number of turtles across time; T234 was admitted once and was then recaptured in 2019. The table is ordered according to turtle entry date.*

Turtle ID	**Entry**	**Release**	**Origin**	**Weight (kg)**	**Bycatch gear**	**State of health upon entry**	**Tagging date**	**Tank size (L)**	**State of health when tagged**
Rosita	NA	NA	NA	78	NA	Healthy	30/01/18	991900*	Healthy
T359	02/01/18	04/03/18	Benicarlo	20.8	Trawl/bottom fishing	Moderate GE	09/02/18	6000	Healthy
"	"	"	"	"	"	"	12/02/18	7210000**	Healthy
T362	16/01/18	06/03/18	Cullera	13	Trawl/ bottom fishing	Moderate GE	09/02/18	3500	Healthy
"	"	"	"	"	"	"	12/02/18	7210000**	Healthy
T396	28/03/18	05/07/18	Vinaroz	22	Trawl/ bottom fishing	Healthy	08/05/18	6000	Healthy
T405	01/06/18	12/07/18	Peniscola	34.24	Trawl/ bottom fishing	Very mild GE	29/06/18	19000	Healthy
T234	30/01/19	*TBC	Burriana	85.5	Trawl/ bottom fishing	Mild GE and fishing hook ingestion	10/10/19	12300	Healthy
T459	25/02/19	26/04/19	Burriana	12.15	Trawl/ bottom fishing	Healthy	05/03/19	3500	Healthy
T476	22/03/19	16/06/19	Vinaroz	15	Trawl/ bottom fishing	Healthy	04/06/19	3500	Healthy
T481	05/04/19	07/06/19	Cullera	25.18	Trawl/ bottom fishing	Healthy	04/06/19	3500	Healthy
T482	11/04/19	03/07/19	Peniscola	30	Trawl/ bottom fishing	Moderate GE	11/06/19	3500	Healthy
T484	26/04/19	02/07/19	Peniscola	13.53	Trawl/ bottom fishing	Mild GE	11/06/19	3500	Healthy

**TBC; To be confirmed.*

Appendix I (Chapter 6)

Sample email (below) and generic research proposal (following page) that were sent to zoos and aquariums for enclosure size data.

Dear [zoo name],

I hope this email finds you well.

I am a PhD student working with Professor Rory Wilson at Swansea University, UK. As part of my PhD, I am comparing the 'step lengths' (i.e., the average distance travelled before changing direction) of free-living animals against enclosure sizes. The goal of this work is to create a metric that could help provide guidance on suitable enclosure sizes for a variety of aerial, terrestrial and aquatic animals (see research proposal attached for more information). Noting that your zoo places animal wellbeing first and foremost, I am sure that you would be interested in helping inform such a study.

I have step length data for a range of wild animals already and would be extremely grateful if you could provide me with the length, width, and area of enclosures in meters for the following animals that my online search has indicated are (or were previously) at [zoo name]:

…

If you have any questions regarding the project please feel free to ask me and if you would like a copy of the work once finished I will be happy to provide it.

Thank you for your time,

Alex Arkwright

P.S. I have attached a list of species that I am collecting enclosure sizes for; I have left space for enclosure sizes to be added if you would like to enter them there. If you have any of the other animals on the list and could provide enclosure sizes for them, I would be extremely grateful.

The Realisable Movement Index: Using straight-line movement path data from free-living animals to inform enclosure size

Abstract

Research deploying logging devices on wild animals has been instrumental to the fields of animal behaviour and movement ecology. Knowledge of animal movement behaviour is crucial when defining species-specific requirements, both in a natural environment and a managed one. Animal care is a top priority for zoos and aquariums, that regularly use animal welfare assessment methods to ensure appropriate nutrition, environmental stimuli and opportunities for behavioural expression. Nonetheless, maintenance of animals in captivity, particularly large vertebrates and the incidence of stereotypic behaviours, often comes under scrutiny.

Understanding the behavioural plasticity already present in free-living animals could help improve the quality of life for conspecifics in captive care as well as help formulate husbandry guidelines. The ability to collect high-resolution data via multi-sensor tags gives researchers the opportunity to study the intricacies of animal movement paths, elucidating the straight-line distance travelled and turning points. Capitalising on high-resolution movement path data, we plan to create 'The Constraint Index', which would incorporate 'step lengths' (i.e., the average distance travelled before turning) and provide guidance on adequate enclosure sizes. In future such a metric could be incorporated into current welfare protocols in order to help maximise animal well-being in captivity.

1. Background

The attachment of multi-sensor tags to wild animals has transformed our understanding of wild animal movement ecology (1-3), behaviour (4-7) and physiology (8, 9). Importantly, an understanding of animal movement (which is often synonymous with animal behaviour) gives researchers powerful insights into effective conservation (10-12), and species-specific behaviours and requirements (1, 5, 12-15). The intricacies of animal movement paths can now be studied in high-resolution, with information on straight-line travel and discrete turn-points reflecting decisions made by animals that are highly relevant for behavioural ecologists (16).

Given that free-living animals tend to display behaviours not seen in captive animals, our knowledge of behavioural ecology in the wild could be used to create environments that encourage a wider range of behaviours in managed care. Whilst it might not make sense or be beneficial for captive animals to display the same behavioural repertoire as wild conspecifics, understanding the behavioural plasticity that already exists in the wild may help improve the quality of life for animals in captivity and help formulate husbandry guidelines to reduce detrimental stereotyped behaviours (see (17-19)). Considering that the maintenance of animals in captivity (particularly large mammals and other vertebrates), is a contentious topic with issues related to well-being, including stress and stereotypic behaviours (20-22), objective welfare measures incorporating wild type behaviours could prove valuable husbandry tools.

Animal welfare is a high priority for zoos, aquaria, and pet owners alike (23). As custodians with control over captive animal management (in terms of environmental surroundings and providing care), it is our duty to ensure the welfare of our animals (19). Appropriate nutrition, environmental stimuli and opportunities for behavioural expression are key to animal wellbeing and mental state (24, 25). Species-specific behaviours must be taken into account if we are to meet the behavioural needs of a species or use behavioural indicators of welfare effectively (see (23, 26-28). Animal welfare assessment methods often utilise resource-based measures, recorded in the animals' environments, and include elements like space, lighting and food requirements, all of which are easily quantifiable and repeatable for individuals and groups (19).

Capitalising on high resolution movement path data, already available from deployments of multi-sensor tags (Daily Diaries, DDs (12); Wildbyte Technologies Ltd., Swansea, UK) on wild animals, we propose a 'Constraint Index' that would incorporate 'step lengths' (i.e., the average distance travelled before changing direction (16)) and could be used to help provide guidance on suitable enclosure sizes for a variety of aerial, terrestrial and aquatic animals.

2. Project aims:

- To investigate the percentage of wild animal straight-line movement paths (step lengths) that can be undertaken in managed care environments.
- To create a metric that could help provide guidance on suitable enclosure sizes for a variety of aerial, terrestrial and aquatic species.

3. Limitations and Perspectives

There are a great many variables that influence animal movement and changes in direction including: resource distribution, obstacles (e.g., bodies of water, rocks and vegetation), social interactions, predators and topography (29-32). Consequently, both free-living and captive animal movement may often not be dependent on innate behaviour drivers; for example, the daily distance travelled by mountain gorillas differs vastly in response to food availability (33). Wild animals often travel large distances, even going days without access to water (30) whereas managed care animals do not. In addition, captive animals are often given enrichment, both structural and nutritional, to encourage activity and to diversify behaviour (23-27). All of these factors can affect animal movement and are beyond the scope of a single study, particularly because captive and wild environments differ substantially.

Nonetheless, free-living animals, despite often having large expanses over which to roam, may conduct various types of relatively short random walks, such as in environments where resource locations are unknown (34). In line with the first aim of this study we are interested in investigating the percentage of wild animal straight-line movement paths that can be undertaken in managed care environments; it is entirely possible that a substantial percentage of step lengths can be undertaken in zoo enclosures. However, if the length of an enclosure only permits a very small percentage of step lengths (say 1-2%) this could indicate that an animal's behavioural needs are not being met; such data could be of use when housing gliding bird species that require added space to manoeuvre (35)).

It is important to recognise that animal enclosures are not designed to be as large as possible but to be suitable and stimulating environments that meet captive animal needs. That said, we believe that comparing step-lengths with enclosure size is of merit and could be used to establish base-line data that could, in future, be incorporated into comprehensive captive welfare guidelines.

4. Research schedule and impacts on participating zoos and aquariums

Wild animal data on step lengths has already been collected and data analysis is underway. Data collection on captive animals enclosure sizes (obtained via email from multiple zoos and aquariums) is also underway.

This work requires the enclosure size in metres for a variety for aerial, terrestrial, and aquatic species (see full list below) currently or previously housed in participating zoos and aquariums. The information would be obtained via email and would only require participating institutions to measure enclosure sizes by hand if blueprints or diagrams with enclosure sizes do not already exist.

Aerial
Andean condor, *Vultur gryphus*
Brunnich's guillemot (or thick-billed murre), *Uria lomvia* (and other murre species)
Fish-eating bat, *Myotis vivesi* (and other bat species)
Imperial cormorant, *Leucocarbo atriceps* (and other cormorant species)
Kittiwake (Black-legged kittiwake, *Rissa tridactyla* or Red-legged kittiwake, *Rissa brevirostris*)
Lesser frigatebird, *Fregata ariel* (and other frigatebird species)
Northern fulmar, *Fulmarus glacialis*
Streaked shearwater, *Calonectris leucomelas* (and other shearwater species)
Red-tailed tropicbird, *Phaethon rubricauda*

Terrestrial
African lion, *Panthera Leo*

Arabian oryx, *Oryx leucoryx*
Chamois, *Rupicapra rupicapra*
Domestic cow, *Bos taurus*
Domestic goat, *Capra aegagrus hircus*
Domestic sheep, *Ovis aries*
European badger, *Meles meles meles*
European beaver (or Eurasian beaver), *Castor fiber*
Ibex, *Capra ibex*
Imperial cormorant, *Leucocarbo atriceps*
Magellanic penguin, *Spheniscus magellanicus*
Red deer, *Cervus elaphus*
Aldabra Giant tortoise, *Aldabrachelys gigantea*
Wild boar, *Sus scrofa*

Aquatic
Imperial cormorant, *Leucocarbo atriceps*
Loggerhead turtle, *Caretta caretta*
Magellanic penguin, *Spheniscus magellanicus*
Sandbar shark, *Carcharhinus plumbeus*
Tiger shark, *Galeocerdo cuvier*
Whale shark, *Rhincodon typus*

5. Significance of the proposed work and plans for publication

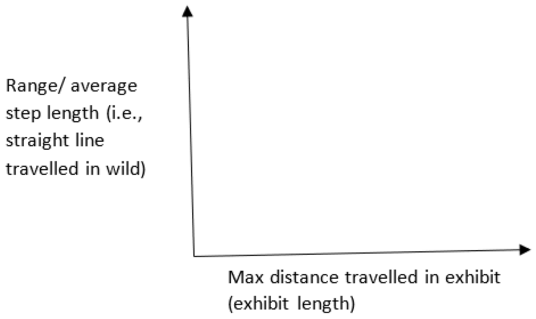
We hope this work will be of use to husbandry efforts globally, both in zoos and aquariums. By creating a metric indicative of adequate enclosure size for a variety of species we seek to reveal whether managed care animals have a sufficient amount of room in which to move or if they might benefit from added space. Our aim from this work is to create an index providing guidance on enclosure size that could be incorporated into current welfare protocols in order to maximise animal well-being in captivity. We intend to submit this work for publication next year after the PhD student has finished defending her thesis. Prior to submission for publication all participating zoos and aquariums will receive a copy of the work. All participating zoos and aquariums have the option to remain anonymous, or feature in the acknowledgements of the paper.

6. Methodology

As mentioned above (see section 3), data on step lengths has been collected and analysed for a variety of aerial, terrestrial and aquatic species. High-resolution data, collected via orientation- and motion-sensitive tags (DDs) provides information on straight-line movement paths (i.e., step lengths) and turning-points which can be quickly analysed via an algorithm devised by Potts et al. (16). For further details regarding how the algorithm functions please see Potts et al. (16).

Enclosure size data will be obtained via email for species in the list above (see section 3), for which step length data exist. Species that are infrequently housed in captivity may be omitted from the list if enclosure sizes cannot be obtained. Participating institutions are asked to measure the enclosure sizes of selected species currently (or previously) housed in their exhibits if blueprints or diagrams with enclosure sizes do not exist. The ‘Zootierliste’ webpage, https://www.zootierliste.de/en/, and websites of zoos and aquariums will be used to gather information on which species are maintained where.

Once collected, data will be used to create 'The Constraint Index' which will incorporate step length and enclosure size and will give an indication of when animals are housed in enclosures of a suitable size and when they might benefit from added space. Various measures of step length (such as the mean, median, mode and range) will be examined and analysed accordingly through qualitative (graphs) and quantitative (statistical) analysis. The results will be used to devise The Constraint Index. The usefulness of this index as an animal welfare tool and its potential implementation will be discussed in the paper.



Persons involved:

- **Primary researcher:** Alexandra Arkwright, PhD research student at Swansea University, UK.
- **PhD Supervisor:** Rory P. Wilson, Professor of Aquatic Biology and Sustainable Aquaculture in the Department of Biosciences, Swansea University, UK.

Researcher signature: [redacted]

Date: 23.09.2021

Supervisor signature: [redacted]

Date: 23.09.2021

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Appendix J (Chapter 6)

Table J1. Summary of care manuals providing enclosure size guidelines for the nine species used in this study. The recommended length x width x height or depth of enclosures was used to estimate the longest length of straight-line travel that they permitted. If care manuals only gave a recommended enclosure area, longest lengths were calculated within rectangular shaped enclosures (twice as long as they were wide) of the recommended area. Abbreviations for enclosure types are as follows: 'min', minimum enclosure size guidelines; 'max', the largest enclosure size recorded during exhibit surveys; 'sing.', 'pair', 'trio' and 'flock', minimum guidelines for a single animal, a pair, a trio and a flock of animals and 'mix', guidelines for a mixed species enclosure (see Chapter 6, Table 4 *notes for explanations of enclosures and remaining abbreviations). Last, the longest length of enclosures was divided by critical step length distances at 50% and 90% limits in the frequency distributions of step lengths (CSL$_{50\%}$ and CSL$_{90\%}$ respectively) to generate two ReMI values (shaded grey). ReMI$_{CSL\_50\%}$ values (lighter grey) that were ≥ 1 and ReMI$_{CSL\_90\%}$ values (darker grey) that were ≥ 0.5 were considered 'adequate' and are in bold.*

Species, Latin name	***Care manual***	***Enclosure type and size guidelines (L x W x H)***	***Longest length (m)***	***CSL $_{50\%}$***	***CSL $_{90\%}$***	***ReMI $_{CSL\_50\%}$***	***ReMI $_{CSL\_90\%}$***
(Aerial species)							
Andean condor, *Vultur gryphus*	AZA Raptor TAG, 2010, *Andean Condor Care Manual*	*^{1}Min 16.5 x 11 x 7.6 Max 30.5 x 24.4 x 30.5	19.8 39.1	1834	12647	0.01 0.02	< 0.01 < 0.01
	CZA Zoos in India, 2014, *Legislation, Policy, Guidelines and Strategy (flying birds)*	*^{2}Sing. 12.7 x 6.3 x 6 Mix. 24.5 x 12.3 x 8 Walk-thr. 200 x 100 x 18	14.2 27.4 223.6			0.01 0.01 0.12	< 0.01 < 0.01 0.02
(Terrestrial species)							
Aldabra giant tortoise, *Aldabrachelys gigantea*	CZA Zoos in India, 2014, *Legislation, Policy, Guidelines and Strategy (Aldabra giant tortoise)*	*^{3}Min 20 x 10	22.4	19	51	**1.2**	0.4
Arabian oryx, *Oryx leucoryx*	AZA Antelope TAG, 2001, *Antelope, Alcelaphinae Husbandry Manual*	*^{4}Sing. 10.6 x 5.3 Pair 12.2 x 6.1	11.9 13.6	30	65	0.4 0.5	0.2 0.2
Domestic sheep, *Ovis aries*	CZA Zoos in India, 2014, *Legislation, Policy, Guidelines and Strategy (wild sheep)*	*^{5}Min 31.6 x 15.8	35.3	49	85	0.72	0.41

	Welsh Assembly Government, 2010, *Code of Practice for the Welfare of Livestock: Sheep* NFACC, 2013, *Code of Practice for the Care and Handling of Sheep*	*[6]Trio 3 x 1.4 Flock 11.8 x 5.9	3.3 13.2			0.07 0.27	0.04 0.16
European badger, *Meles meles meles*	AZA Small Carnivore TAG, 2010, *Mustelid, Mustelidae Care Manual*	*[7]Min 7.7 x 3.9	8.6	40	277	0.21	0.03
(Aquatic species)							
Imperial cormorant, *Leucocarbo atriceps*	CZA Zoos in India, 2014, *Legislation, Policy, Guidelines and Strategy*	*[8]Mix. 11 x 5.5 x 1.5	12.3	50	131	0.25	0.09
Loggerhead turtle, *Caretta caretta*	Higgins BM, 2002. Sea turtle husbandry. Pages 411-440. *The Biology of Sea Turtles, Volume II*	*[9]A 16.9 x 8.4 x 1.3 B 21.1 x 10.6 x 2.1 C 20.3 x 10.2 x 1.4	18.9 23.6 22.7	19	43	0.99 **1.24** **1.19**	0.44 **0.55** **0.53**
Magellanic penguin, *Spheniscus magellanicus*	AZA Penguin TAG, 2014, *Penguin (Spheniscidae) Care Manual*	*[10]Min 2.5 x 1.3 x 0.9	2.8	72	182	0.04	0.02
Whale shark, *Rhincodon typus*	Smith et al. 2004. *The Elasmobranch Husbandry Manual: Captive Care of Sharks, Rays and Their Relatives*	*[11]OEA. 27 x 12 x 3.5	29.5	131	1676	0.23	0.02
	Smith et al. 2017. *The Elasmobranch Husbandry Manual II: Recent Advances in the Care of Sharks, Rays and Their Relatives*	*[11]AA. 70 x 30 x 9.25 GA. 78 x 33 OAK. 34 (max) x 9 OCA. 35 × 27 × 10	76.2 84.6 34 44.2			0.58 0.64 0.26 0.34	0.05 0.05 0.02 0.03

Continued.