Environmental determinants for repeatability of activity patterns in free-ranging elasmobranchs


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Submitted by

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Declaration

I declare this thesis as my own account of my research and contains as its main content work which has not been previously submitted for a degree at any tertiary education institution.

Rachel Newsome

[redacted]

Abstract

Repeatability of behaviour is the degree of behavioural variation attributed to differences between- or within- individuals in a population and may often be conceptualised as animal personality. Behaviour is often plastic in response to environmental challenges to maximise individual survival. In ectotherms, this may be expressed as changes in behaviours due to higher environmental temperatures increasing metabolic demand. Personality is thought to constrain this behavioural plasticity as individuals express behaviours within their personality type. Most studies in this field have been conducted under controlled or semi-controlled conditions, which control for confounding factors and hence remain limited in their applicability in the face of uncertain field conditions. To date, no field studies have focused on the environmental conditions that determine how repeatability of behaviour is exhibited. Here we use biotelemetry tag derived activity data to assess environmental factors influencing the repeatability of activity patterns (i.e., repeated behaviours) in two euryhaline free-ranging elasmobranchs with differing life histories; the largetooth sawfish (*Pristis pristis*) and bull shark (*Carcharhinus leucas*) in the Fitzroy River. In response to increasing environmental temperatures and metabolism across the study period, between-individual repeatability of behaviour varied in sawfish, but not bull sharks. Overall between-individual repeatability of behaviour increased across the study period as sawfish altered their behaviours presumably to mitigate competition. Between-individual repeatability of behaviour decreased across the study period with respect to diurnal activity rhythms, indicating sawfish became less diurnal in their activity use. This may indicate active avoidance of the hottest part of the day and a loss to individuals' ability to temporally partition the diel cycle, with more overlap in activity apparent in the population. Additionally, individuals showed consistent individual differences in their within-individual repeatability of behaviour. This further supports the hypothesis that individuals of these species exhibit personalities. Ecological pressures such as competition, predation pressure and resource constraints are potential drivers of the formation of personality, both in this system and in general. This study demonstrates that repeatability of behaviour can be studied in the field using acoustic telemetry. Additionally, this approach can be used to understand the effects of environmental change on specialisation in other aquatic ectotherms.

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1 Introduction

Naturally, many environments experience constantly changing conditions, and the animals that inhabit these environments generally possess behavioural and physiological strategies to maximise their individual fitness in the face of these changes (Beever et al. 2017). Behavioural flexibility (i.e., the capacity of an individual to change its behaviour in response to varying environmental conditions (Hadfield et al. 1996)) is an important component of determining the resilience of species in the face of environmental disturbance (see Buchholz et al. 2019). Behavioural flexibility can provide species with the necessary tools to mitigate some of the negative effects of environmental change expected to occur as a result of the Anthropocene (Buchholz et al. 2019). For example, behavioural flexibility in response to the environment can be seen through behavioural thermoregulation of oscillatory diving in blue sharks (*Prionace glauca*), who spend periods of time in warmer surface waters after diving to depth, which is thought to be a response to recover heat loss (Klimley et al. 2002). As such, behavioural flexibility may provide species with the mechanisms to respond to environmental changes. In the face of changing climatic conditions, this flexibility may be pivotal in predicting susceptibility of species to climate-change related biodiversity threats (Huey et al. 2012; Mason et al. 2014; Moritz et al. 2013; Muñoz et al. 2015; Sunday et al. 2014). Despite this, little is known about each individuals' behavioural flexibility, and as such, their capacity to respond to environmental variation. Given the rapid rate that environments are expected to change over the next few decades (see Hoffmann et al. 2011), it is important to understand species' behavioural flexibility, and as such, their resilience to environmental threats, such as climate change (Buchholz et al. 2019).

Behavioural flexibility, though advantageous in allowing animals to adjust to different environmental conditions, is likely not limitless. One factor that can constrain behavioural responses is an individuals' personality. Animal personality is the long-term, stable behavioural differences among individuals (Carere et al. 2011) and has been seen to occur in a number of taxa, including mammals, reptiles, fish, birds, amphibians, molluscs and arthropods (Gosling 2001). Personality may limit behavioural flexibility by constraining an individuals' behaviours into their broad personality categories. For example, an individual that demonstrates a bold personality would be expected to remain bold across contexts and a shy individual would be expected to remain shy across contexts. This personality trend may have survival implications as bold, exploratory individuals may see greater foraging efficiency and resource acquisition but may suffer from increased chance of predation due to greater exposure during foraging and exploration (see Dhellemmes et al. 2020; Moiron et al. 2020). Alternatively, shy individuals are likely to prioritise refuge, so have reduced chance of predation but also reduced competitive ability and resource acquisition. Personality, however, is known to be driven by how individuals respond to intra- and inter-specific competition, ecological opportunity, and predation risk (Smith et al. 2008; see also Dhellemmes et al. 2020). As individuals with different personalities may be better adept at refuge or foraging, some personalities may be more resistant to change. In a changing environment with low predation risk and decreasing resources, bold individuals are likely to be more resistant to change as they are able to acquire resources more efficiently (Careau et al. 2008). However, shy personalities may be beneficial in environments with high predation risk and decreasing resources, as they do not need to meet the same energetic requirements as bold individuals (see Daan et al. 1990; Hammond et al. 1997) and may be able to mitigate chance of predation by reducing exposure and prioritising refuge (Careau et al. 2008).

Another factor that constrains behavioural flexibility in animals is their metabolic rate. Individual metabolism contributes the largest portion of an individuals' daily energy expenditure, with consumption rates and foraging needs directly proportional to metabolic demands (Whitney et al. 2016). Variation in metabolic rate may arise from inherent differences between organisms' physiology, resulting from diversity in their ecological demands (Whitney et al. 2016). Individuals must meet their metabolic demands, otherwise will suffer from loss of body condition or mortality through starvation (Loehr et al. 2007; Wikelski et al. 2000; Xu et al. 2010). The constraints placed on the behaviours of animals by metabolic rate are further complicated by the intrinsic link between metabolism and personality. Certain behaviours may consume – or help gain – energy at varying rates; with foraging behaviours causing net energy gain and exploratory or aggressive behaviours depleting energy from the metabolic system (Biro et al. 2010b). This pattern is seen through a positive feedback loop; for example, bold personalities are more active and hence have higher energy requirements and a greater demand for food acquisition. As such, individuals with higher energetic demands must forage more frequently and may have less capacity to adjust their behavioural (i.e., activity) patterns.

The link between behaviour and metabolism, and the factors influencing the metabolic rate of an individual, are particularly relevant in ectothermic organisms, whose physiological performance is heavily influenced by body temperature, which is dictated by ambient temperatures (Angilletta Jr et al. 2002). Most fishes are aquatic ectotherms and typically demonstrate direct, positive exponential relationships between metabolic rate and temperature (Gillooly et al. 2002). For instance, a 10ºC increase in environmental temperature generally doubles or triples the basal or standard metabolic rates of these organisms (Carlson et al. 2004; Clarke et al. 1999; Gillooly et al. 2002; Schmidt-Nielsen 1997). As a consequence, if temperatures increase, ectothermic organisms must increase energy intake by foraging to maintain body condition and growth during these new temperature regimes (Lear et al. 2020).

Additionally, many ectotherms also utilise varying temperatures in their environment for behavioural thermoregulation, ‘shuttling’ to warmer waters to maximise physiological performance during foraging (e.g., Hopkins et al. 1994; Sims et al. 2006) or even spending greater periods of time in warmer temperatures when pregnant to reduce the duration of gestation (Economakis et al. 1998; Hight et al. 2007; Wallman et al. 2006). The capacity for behavioural flexibility in response to changing environmental temperatures is further limited by the increasing need to forage with increasing ambient temperatures. Individuals focus more on meeting new energetic demands under these scenarios, resulting in reduced capacity for behavioural flexibility and more risk-prone behaviours (Lienart et al. 2014). The impact ambient temperature has on ectotherm physiology and behaviour extends into animal personality with small (< 3ºC) temperature changes in the environment having impacts on fish behaviour, resulting in increases to the personality traits of activity and boldness by a factor of 2.5 to six (Biro et al. 2010a).

While it is clear that the environment can have profound effects on animal personality, to date research has primarily focused on controlled or semi-controlled conditions through the use of laboratory or enclosed open-field tests. Under controlled conditions, individuals are usually tested for sociability and a ‘novel open-field assay’, where individuals are allowed access to a novel open-field. Here behaviours, such as emergence, exploration, and number of sectors within novel open-field visited, are recorded. Exploration is often considered as the rate of movements of an individual within the novel open-field; the number of sectors within the field that the individual visits per minute (Dhellemmes et al. 2020). These controlled studies (e.g., Biro et al. 2010b; Dhellemmes et al. 2020) have provided the foundation for animal personality research and overcome the myriad of logistical complexities associated with field studies (Réale et al. 2007). However, many abiotic and biotic factors that limit animal behaviours (e.g., predation risk, foraging requirements) and their interactive influence are not easily replicated in such experiments. Field studies provide insight into the natural relationships between personality, physiology, and environment and how these may have implications for individuals’ survival under changing conditions. As behavioural flexibility is how animals respond to environmental challenges (Hadfield et al. 1996) and personality may limit this response (see Careau et al. 2008), field studies are pivotal in determining how personality may limit specialisation and behavioural flexibility in the face of extreme environmental change and might provide a valuable addition to controlled laboratory experiments.

Despite the importance of measuring personality in the wild, data has been difficult to obtain (see Réale et al. 2007). Acoustic telemetry is a method of attaching transmitters to animals in order to remotely track and collect movement data (Rodgers et al. 1996) and recent advances in this field have enabled remote data collection of the environment, behaviour, and physiology of animals (Wilmers et al. 2015). Animal-attached biotelemetry tags provide an avenue for the quantification of activity of wild animals in the field. Specifically, accelerometers, a type of sensor included in some biotelemetry and bio-logging devices, are able to record body movement at sub-second sampling rates, which can be used as a proxy for activity and behaviour (Shepard et al. 2008; Wilson et al. 2006a). Since activity levels strongly correlate with boldness/shyness, activity in turn can be used as a proxy for personality (Dhellemmes et al. 2021).

Here, biotelemetry derived acceleration data were used to assess how environmental factors influence the repeatability of behaviour (i.e., personality) in a field environment.

Importantly, data were collected from two euryhaline free-ranging elasmobranchs with contrasting lifestyles; the largetooth sawfish (*Pristis pristis*) and the bull shark (*Carcharhinus leucas*) in the Fitzroy River, north-Western Australia. The Fitzroy River experiences extreme changes to environmental conditions between seasons, particularly with reference to water temperatures (CSIRO 2018). The increasing metabolic demands as a result of increasing temperature put considerable pressure on ectothermic predators in this system as they are faced with a concomitant decline in resource density during the time of rising temperatures (Lear et al. 2020). As a result of the extreme seasonal changes, this system provides an important opportunity to study the environmental determinants of personality. Additionally, comparing how repeatability of behaviour varies in two species with divergent lifestyles; the benthic, inactive largetooth sawfish compared to the pelagic, active bull shark, may provide insight into how species with differing lifestyles and associated metabolic demands may cope with changes to their environment. Specifically, this study aimed to determine: (i) how repeatability of behaviour exhibits itself in a completely natural field environment and (ii) how repeatability of behaviour may vary with changing environmental conditions. Given that an increase in metabolism correlates to an increase in activity, repeatability of behaviour was expected to decrease as individuals lose their specialisation to the environment and become more physiologically stressed across the study period. Additionally, it was expected that the pelagic lifestyle of the bull shark may constrain its personality and behavioural flexibility in this environment.

2 Materials and methods

2.1 Study species and region

This study was undertaken in the freshwater reaches of the Fitzroy River (17º33’12”S, 123º35’20”E), which flows through the Kimberly region of Western Australia (Figure 2.1).

The Fitzroy River is exposed to a monsoonal dynamic climatic environment that experiences distinct changes in evaporation, precipitation, and temperature between wet and dry seasons (CSIRO 2018). Mean annual rainfall and potential evaporation range from 400 to 1000 mm and 1900 to 2050 mm, respectively. Precipitation is largely limited to the wet season (November to April), with 93% of annual rain falling during this six-month period (CSIRO 2018). During this period, the river is generally connected and flowing. Air temperatures are lowest at the start of the dry season and begin to increase from early in the dry season until the wet season, with temperatures exceeding 37ºC common from August (CSIRO 2018). As temperatures start to increase during the dry season, so does evaporation, causing river flow to decrease. Discharge and river stage height progressively lessen until the river becomes a collection of disconnected, isolated pools (CSIRO 2018; Whitty et al. 2017). All sampling occurred in these inland, freshwater pools during the dry season (May to October).

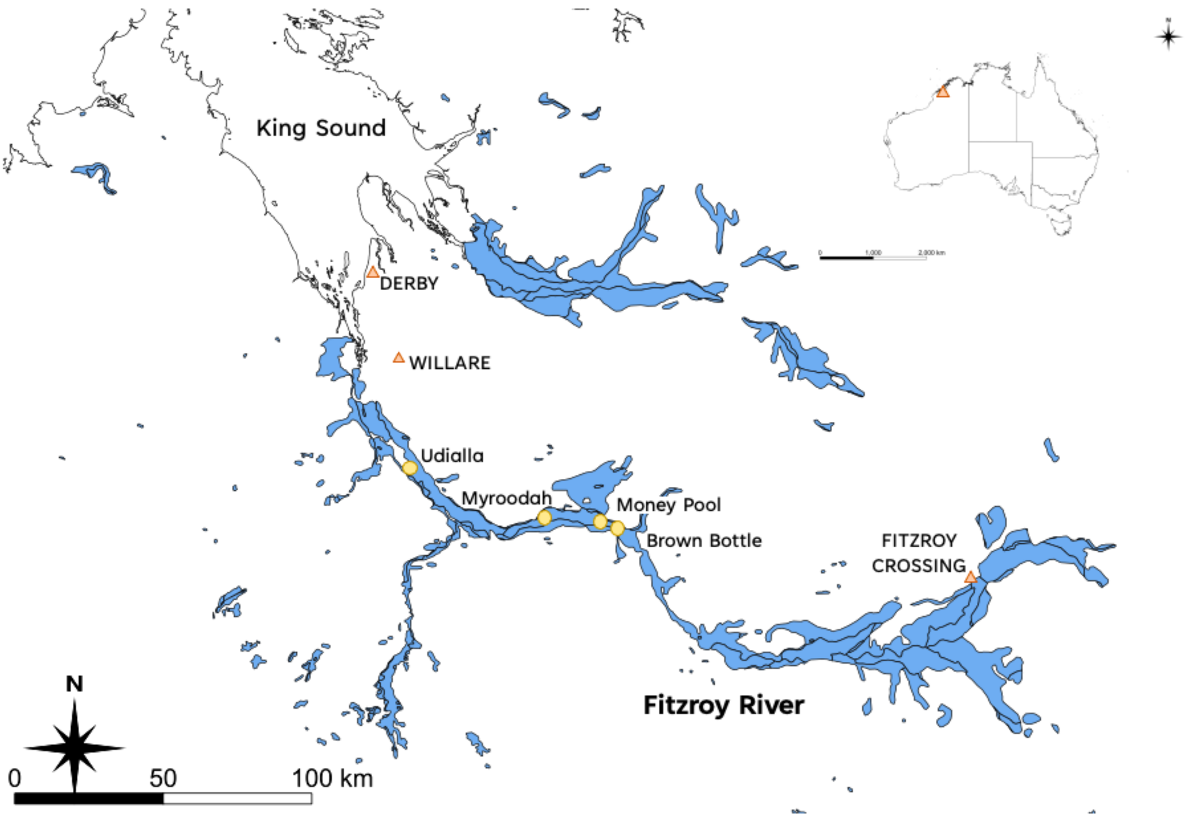

Figure 2.1: Location of the Fitzroy River and associated study sites, north-western Australia. Map amended from Lee (2021, unpublished).

The Fitzroy River, amongst other northern Australian rivers, acts as a nursery habitat for juvenile bull sharks and largetooth sawfish and is the last known intact nursery ground for the largetooth sawfish (Morgan et al. 2011). Sawfish use the freshwater reaches as a nursery for between four and six years, reaching total lengths of 2.2 to 2.6 m before returning to marine environments to mature (Thorburn et al. 2007; Whitty et al. 2017; Whitty et al. 2009). Juvenile bull sharks are thought to remain in these rivers for up to four years (Thorburn et al. 2008). As ectotherms, both species’ metabolism is determined by body temperature, which in turn is dependent upon surrounding temperatures (Angilletta Jr et al. 2002). As a result, the metabolic rate of the individuals in this system vary with seasonal temperature changes. Warmer temperatures typically provide benefits for ectotherms with many species utilising warmer environments to undertake thermoregulatory behaviours such as ‘shuttling’ into warmer waters to optimise physiological processes (Casterlin et al. 1979; Hopkins et al. 1994; Sims et al. 2006). However, the increased energy demands that result from warmer temperatures can provide considerable stress if energy intake is limited, through e.g., insufficient prey availability or other ecological processes limiting access to required resources. In this system, as the dry season commences environmental temperatures and metabolic rates of individual sharks and sawfish rise, putting individuals under increasing physiological stress as their energetic demands are not met, resulting in a loss of body condition (Lear et al. 2020). The environmental changes and associated physiological pressures placed on the animals in this system makes it a model site for studying the relationship between ecophysiology and behaviour, particularly how repeatability of behaviour may be influenced by varying environmental conditions.

2.2 Capture and tag deployment

Juvenile and sub-adult bull sharks and largetooth sawfish were caught via gillnet (152-202 mm stretched mesh) from 2015-2019. Gillnets were deployed during the day and night, and checked every 1-2 hours, depending on bycatch levels. After capture, fish were removed from nets, sexed, measured for total length (TL) and girth (taken from the armpit of the pectoral fin) and double-tagged with both V13AP (Figure 2.2) and V13T acoustic transmitters (Vemco, Innovasea, NS, CAN). Tag attachment method differed between 2015 and 2016-2019. In 2015, tags were externally attached to the dorsal fin of the animals. In 2016, tag attachment was changed to increase tag retention rates. First, animals were placed into tonic immobility, a coma-like state, to minimise movement (Brooks et al. 2011) and enhance ease of surgery. Tags were then surgically inserted into the peritoneal cavity via an incision made anterior to the pelvic fins. Tags and all surgical instruments were disinfected by bathing in betadine prior to surgical implantation. After implantation, incisions were closed with 2 to 3 interrupted sutures, using Monosyn absorbable monofilament (Q310 MonoWeb, Patterson Veterinary, Devens, MA, USA). Once animals were released, tag transmissions were recorded via a network of one to five acoustic receivers deployed in each pool (VEMCO VR2W; Figure 2.1), which were serviced and downloaded semi-annually throughout the duration of the study. Detection range reached up to 400m at 95% detection probability (Whitty et al. 2009). Tags had a battery life of approximately 250 days. All work involving animals was conducted in compliance with Fish Resources Management Act 1994 exemption and Murdoch University Ethics permit [RW2757/15].

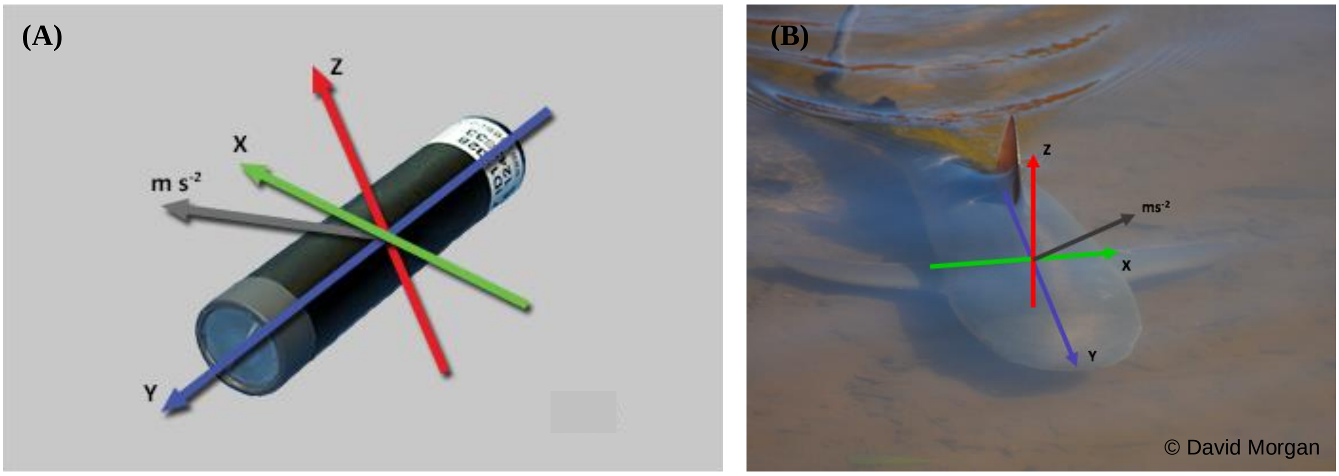

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Figure 2.2: (A) Vemco V13AP coded transmitter surgically implanted into bull sharks and largetooth sawfish and (B) bull shark with arrows showing the three axes acceleration is collected from; Z (sway), X (surge) and Y (heave). Grey arrow represents VeDBA. Figure modified from Innovasea (2018).

Combined, tags recorded triaxial acceleration (V13AP), pressure (i.e., depth) (V13AP) and temperature (V13T). Tags recorded and transmitted data at a random delay centred around two minutes. V13AP tags alternately transmitted acceleration and depth. Acceleration was sampled at a frequency of 10 Hz for a 20-second period, and a single mean value from this period was transmitted, whereas depth and temperature were instantaneously recorded and transmitted. All acceleration data was recorded as vectorial dynamic body acceleration

(VeDBA), which was calculated on-board tags before data transmission via the following equation,

$$VeDBA = \sqrt{(A_{Xt} - G_{Xt})^2 + (A_{Yt} - G_{Yt})^2 + (A_{Zt} - G_{Zt})^2} \qquad (1)$$

where A_X, A_Y and A_Z are raw acceleration and G_X, G_Y and G_Z are gravitational acceleration, observed at time t for each orthogonal body axis (Innovasea, 2018, Figure 2.2). The maximum VeDBA tags were able to record was 4.901 ms^{-2}.

2.3 Data analyses

All analyses were conducted in R (version 3.5.1) (R Core Team, 2013).

2.3.1 Activity

To reduce bias resulting from inconsistency in times sampled (i.e., overrepresentation of night- or daytime sampling units), all data was resampled into daily activity. Daily activity (i.e., data from each 24-hour cycle) was determined as an appropriate sampling unit as it overcame this bias, was viable due to the large temporal timeframe data was collected over in this study, and also encompassed daily cycles of activity and inactivity.

Bull sharks and largetooth sawfish are two elasmobranchs with differing lifestyles. Bull sharks are pelagic species that are obligate ram ventilators that need constant water flow over their gills in order to breathe. As such, they do not cease swimming, so states of ‘rest’, or relative inactivity, are difficult to discern (Crear et al. 2019). Largetooth sawfish, in comparison, are a demersal species that forage near the riverbed. This demersal lifestyle, and the associated periods of immobility as part of their feeding strategy, means that sawfish are able to respire via buccal pumping (i.e., drawing water over their gills manually) which can be viewed as inactivity (i.e., 'rest') (Kelly et al. 2021). Some behavioural studies classify data as binary for easier interpretation (e.g., Rutter et al. 1997), so to ensure that interpretation of activity patterns were consistent between individual sawfish, sawfish acceleration data (VeDBA) were converted into binary form prior to further analyses. Largetooth sawfish VeDBA values were first processed using histogram segregation for each individual to segregate VeDBA into activity levels. A bimodal frequency distribution of VeDBA confirmed periods of inactivity (see Appendix 1). The first 'peak' of frequent but low VeDBA values represented when individuals were inactive. VeDBA values greater than the trough between peaks were assumed to represent times when individuals were active (i.e., swimming). The lowest frequency VeDBA value between the two peaks was determined as the threshold to determine active or inactive states (Appendix 1). To obtain a binary dataset, all VeDBA values below (i.e., 'resting state') and above (i.e., 'active state') this threshold were converted into 0s and 1s, respectively. Because bull sharks are obligate ram ventilators and unable to fully rest like largetooth sawfish, histogram segregation could not be implemented for this species. In bull sharks, by comparison, there was no bimodality present in the frequency distribution (see Appendix 2) and as such, raw VeDBA data were used for analyses for this species.

Acoustic telemetry as a method of data collection can produce temporal biases, as a result of incomplete datasets. An animal must be within the detection range of a receiver in order for a tag transmission to be recorded, and so continuous time-series of data are rarely obtained (Winton et al. 2018). This issue remains present, despite the 95% detection probability as a result of very high receiver coverage in dry-season pools (i.e., 95% of all transmission made by tags are logged by receivers) in this study system (see Whitty et al. 2009 for details of receiver array and coverage). As such, more detections may occur during certain times of the day, consequently over-representing that time of day in the dataset. For example, if there were more detections during the daytime than nighttime, this would underestimate true activity as the daytime is over-represented in the dataset (assuming individuals are more active at night). This may be problematic for data interpretation, as temporally biased activity patterns would inhibit the ability to determine true repeatability of behaviour. To overcome this issue, raw daily VeDBA was standardised into mean activity levels occurring during the daytime and nighttime of each day, ensuring that certain times of the day would no longer be over- or under-represented. This method was termed ‘standardised daily activity’, and was calculated using the following equation,

$$P = \frac{N_{DAY}.\overline{Time_{DAY}^{ACTIVE}} + N_{NIGHT} \bullet \overline{Time_{NIGHT}^{ACTIVE}}}{N_{DAY} + N_{NIGHT}} \qquad (2)$$

where N_{DAY} and N_{NIGHT} refer to the number of hours during the daytime and nighttime, respectively. This was determined based on the average sunset and sunrise times at the study site during the year. $\overline{Time_{DAY}^{ACTIVE}}$ and $\overline{Time_{NIGHT}^{ACTIVE}}$ refer to the mean activity (i.e., VeDBA) during the daytime and nighttime, respectively. Average sunset and sunrise times were estimated based on sunset and sunrise times sourced from WillyWeather (www.sunrisesunset.willyweather.com.au) for the site Willare (Figure 2.1), which is located approximately 100 km north-west from the pools where sharks were tagged and tracked.

2.3.2 Diurnality and crepuscularity indices

Activity rhythms, such as circadian rhythms, are an important component of environmental adaptation that allow the individuals' internal processes to occur in concert with daily environmental changes (Aschoff 1981). Locomotory activity in fishes is known to exhibit daily rhythms that correlate with light levels (Thorpe 1978). To understand how individuals distributed their activity throughout the diel period, diurnality and crepuscularity indices were developed. The diurnality index calculates relative activity levels during daylight hours, compared to the rest of the 24-hour period (Bonnot et al. 2020). Index values range from 0 to +1, where larger values equate to higher activity levels occurring during the diurnal period of interest (i.e., the daytime, rather than nighttime) (Ensing et al. 2014). The diurnality index was calculated for each day according to the following equation,

$$D_i = \frac{\overline{A_{Day}}}{\overline{A_{DAY}} + \overline{A_{NIGHT}}} \tag{3}$$

where $\overline{A_{DAY}}$ is the mean activity value during the daytime and $\overline{A_{NIGHT}}$ is the mean activity value during the nighttime (Bonnot et al. 2020).

To gain further understanding into the acute temporal changes in activity, crepuscularity was also calculated as a crepuscularity index. This is similar to a diurnality index, except that it calculates relative activity levels during twilight periods (i.e., dawn and dusk). To do this, two crepuscularity indices were estimated using the following equations,

$$C_{i_{dawn}} = \frac{\overline{A_{DAWN}}}{\overline{A_{DAWN}} + \overline{A_{DAY}} + \overline{A_{DUSK}} + \overline{A_{NIGHT}}} \tag{4}$$

$$C_{i_{dusk}} = \frac{\overline{A_{DUSK}}}{\overline{A_{DAWN}} + \overline{A_{DAY}} + \overline{A_{DUSK}} + \overline{A_{NIGHT}}} \tag{5}$$

where $C_{i_{dawn}}$ is the dawn crepuscularity index, $C_{i_{dusk}}$ is the dusk crepuscularity index, and $\overline{A_{DAWN}}$ and $\overline{A_{DUSK}}$ are the mean activity value during dawn and dusk of any day, respectively. Dawn and dusk were defined as the two-hour window centred on the mean sunset and sunrise times for Willare (Bonnot et al. 2020).

2.4 Statistical analyses and model selection

To determine the appropriate period (i.e., days elapsed) that should be used to calculate repeatability, an elbow plot of standardised daily activity, diurnality and crepuscularity indices was calculated. Mean repeatability (i.e., standard deviation or intraclass correlation coefficient) of time periods from two to ten days was calculated and plotted. The period that allowed highest resolution of results while simultaneously minimising variation was determined as the point immediately following the largest change in repeatability (i.e., elbow). The ideal period was determined as four days for all metrics, based off the elbow occurring at four days (Appendix 3).

2.4.1 Between-individual variation

To test between-individual variation in repeatability of behaviour, an intraclass correlation coefficient (ICC) was used. The ICC is a statistical value, generally ranging from 0 to 1, that is used in medical, psychological, biological, and genetic studies to estimate the degree of correlation within repeated measurements of a class of data (Liljequist et al. 2019). When individuals are distinct from each other but have similar patterns of behaviour within themselves (Figure 2.3A), ICC will be closer to 1. When individuals demonstrate similar behaviour patterns (Figure 2.3B), ICC is closer to 0. ICCs were calculated using the *icc* function from the *irr* package (Gamer *et al.*, 2012). Values for standardised daily activity or diurnality index were included to obtain the ICC for that window (i.e., four-day period). The ICC for each window were then collated for the entire study period for each species. Negative ICC values are considered unreliable (Lahey et al. 1983) and were removed prior to further analyses.

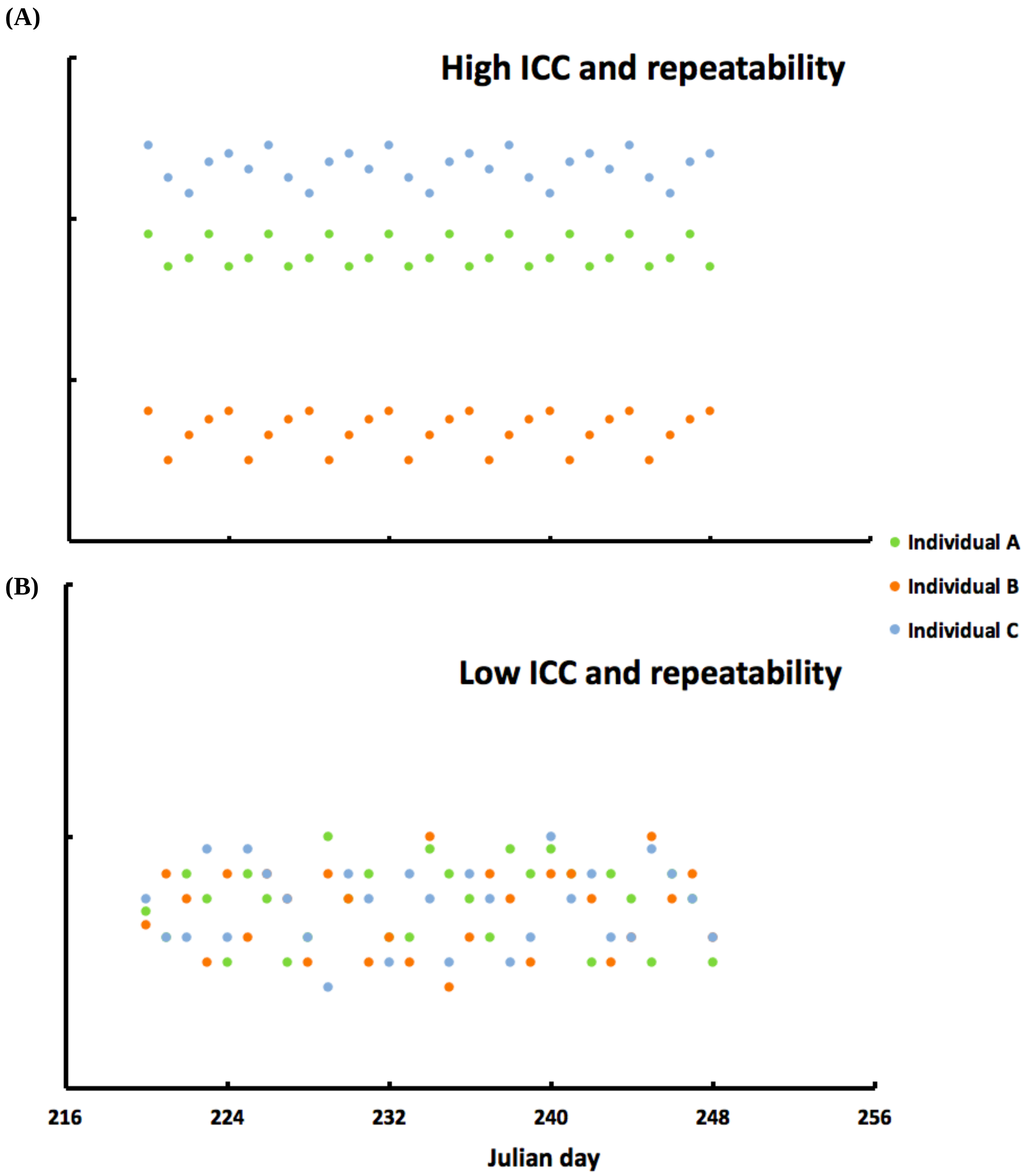

Figure 2.3: Schematic visualisation of activity patterns of (A) three individuals that are closely correlated within themselves but distinct from each other and (B) three individuals that do not follow any patterns within themselves but are closely correlated between each other. Data is used to visualise how patterns in a dataset may result in certain ICC or repeatability. (A) would show high within-individual ICC and repeatability; all individuals are repeatable within themselves. (B) would show low within-individual ICC and repeatability; individuals do not show a high degree of repeatability within themselves.

To assess how variation in environmental conditions affected ICC values, linear models were fitted using the *lm* function from base R. Modelling was done separately for bull sharks and largetooth sawfish. The properties of the data meant that a change in the day of the year was colinear to changes in a number of other key variables including day length, temperature, and body condition of individuals in the system. As a result, Julian day was the only predictor variable that could be included in these models examining between-individual variation. Julian day is a chronological, consecutive sequences of numbers since the start of a Julian period. In this case, the Julian period is the year and Julian day represents the days of the year, beginning on July 1st (i.e., 182) and ending of December 31st (i.e., 365). In these models, Julian day represented changes to the environment (i.e., day length, temperature) and individuals' physiology (i.e., metabolism, energetic requirements, body condition) through the study period. An F-test was used to test the significance between each model and its respective null model, and to determine the model of best fit. A p-value of ≤ 0.05 was used to test for significance.

2.4.2 Within-individual variation

To further understand the factors driving changes in between-individual repeatability (i.e., ICC values), how within-individual variation changed in response to environmental and biological factors was examined. Within-individual repeatability of behaviour was termed 'consistency' and is a measure of how consistent behaviours are within each individual over a given time period. Consistency was calculated as the standard deviation of standardised daily activity, diurnality and crepuscularity of each individual across four-day windows.

Linear mixed-effect models (LMMs) were used to determine environmental and biological factors affecting within-individual variation. LMMs were calculated using the *lmer* function from the *lme4* package (Bates *et al.*, 2021). Some individuals did not have sex data and the *lmer* function is unable to handle missing data (i.e., NA's). As such, individuals where NA's were present in the dataset were excluded. LMMs were fitted separately for standardised daily activity, diurnality and crepuscularity indices for each species. LMMs were made with individual ID as a random effect and standard deviation (i.e., consistency) as the fixed effect. Potential explanatory variables included continuous variables of Julian day, mean daily temperature, and total length and categorical variables of year, sex, lunar phase, and location (Table 2.1), as well as an interaction between mean daily temperature and location. Mean daily temperature was calculated from each individuals' tag data. Because temperature data for bull sharks from 2015 was not available, temperature from sawfish occupying the same pool was used. The *dredge* function from the *MuMIN* package (Bartoń, 2020) was used for model selection using parsimony. The model that explained most of the variation in the data using fewest predictor variables was chosen on the basis that it had better predictive ability. This was selected for using Akaike information criteria, standardised for small datasets (AICc). Once final models were established, the percentage variation that the random effect of ID had on each model was determined as $\frac{Variance_{ID}}{Variance_{residual}}$ from each model output.

Table 2.1: Potential explanatory variables used for modelling drivers of within-individual variation (i.e., consistency).

Explanatory variable	**Type**	**Units**	**Source**
Julian day	Continuous	Day of year	Vemco transmitter
Mean temperature	Continuous	ºC	Vemco transmitter
Year	Categorical	Year	Vemco transmitter
Sex	Categorical	NA	Field observations
Total length	Continuous	cm	Field observations
Lunar phase	Categorical	NA	*Calculated
Location	Categorical	NA	Vemco receiver

*Calculated using dates sourced from Vemco transmitters, calculated as the lunar phase centred on midnight of the first day of each four-day window

3 Results

3.1 Deployments

Eleven bull sharks and 19 largetooth sawfish were tracked from 2015 through 2019. Six individuals (five bull sharks, one sawfish) died within the study period, indicated by acceleration data for an individual flat-lining around 0 ms^{-2}. These individuals were removed from the dataset. For individuals that died but remained with sufficient data (haphazardly determined as > 55 days), all data after determined death points were removed for each individual prior to further analyses. Individual tags were deployed between July (Julian day 182) and mid-August (Julian day 226) from a range of pools within the study site, though most individuals were captured in pools ‘Money’ and ‘Myroodah’ (Table 3.1). Individuals yielded between 56 and 187 days of data, though no individual bull shark data exceeded 100 days (Table 3.1). Number of detections for individuals ranged from 11,848 (ID = 1) to 28,374 (ID = 11) and 18,625 (ID = 16) to 61,391 (ID = 8) detections in bull sharks and sawfish, respectively (Table 3.1). Raw bull shark data was reduced from 16,622 data points to 326 data points for standardised daily activity and 99 data points for diurnality index and raw sawfish data was reduced from 22,711 data points to 154 data points for standardised daily activity and 132 data points for the diurnality index (Figure 3.1). Water temperature increased across the study period from July to October, then plateaued from October until December (Appendix 4). Mean water temperatures experienced by individuals ranged from 20.847 ºC to 33.463 ºC across the study period (Figure 3.2). However, temperature varied slightly between pools and between years. Individual temperature ranges were between 9.802 and 15.234ºC, with a mean temperature range of 12.714ºC (Table 3.1).

Table 3.1: Metadata for all bull shark (*C. leucas*) (n = 11) and largetooth sawfish (*P. pristis*) (n = 19) used for data analysis in this study. Metadata includes identification number, year of data collection, sex, total length (cm), Fitzroy River 'pool' location, Julian day of capture and tag deployment, mean overall vectoral dynamic body acceleration (VeDBA) (ms^{-2}) ± standard deviation, minimum and maximum pool temperature, number of detections and days of detection for each individual.

Bull shark (*Carcharhinus leucas*)										
ID	**Year**	**Sex**	**Total length (cm)**	**Location (pool)**	**Julian day when deployed**	**Mean VeDBA ± SD (ms^{-2})**	**Minimum pool temperature (ºC)**	**Maximum pool temperature (ºC)**	**Number of detections**	**Days of detection**
1	2015	Male	740	Myroodah	218	0.372 ± 0.466	22.117	34.244	11,848	92
2	2015	*NA*	840	Myroodah	226	0.739 ± 0.475	22.117	34.244	16,622	100
3	2015	*NA*	797	Myroodah	226	0.756 ± 0.466	22.117	34.244	16,309	91
4	2015	Female	1362	Brown Bottle	226	0.584 ± 0.328	22.117	34.244	25,392	68
5	2016	Female	860	Money	196	0.716 ± 0.402	19.286	31.193	11,924	92
6	2016	Male	870	Money	196	0.626 ± 0.430	19.354	31.311	22,812	57
7	2016	Male	1481	Money	196	0.494 ± 0.291	19.331	30.603	16,431	92
8	2016	Female	830	Myroodah	197	0.860 ± 0.471	20.075	31.702	27,364	74
9	2016	Female	980	Myroodah	197	0.655 ± 0.495	20.108	32.184	27,691	91
10	2016	Male	802	Brown Bottle	199	0.727 ± 0.374	19.835	31.417	26,346	89
11	2016	Female	948	Myroodah	199	0.701 ± 0.348	19.306	31.452	28,374	88
Largetooth sawfish (*Pristis pristis*)										
1	2015	Male	2191	Myroodah	219	1.056 ± 1.352	22.117	34.244	24,625	135
2	2015	Female	2551	Udialla	224	0.434 ± 0.679	21.531	31.333	19,903	69

3	2016	Female	2570	Myroodah	197	0.410 ± 0.518	20.150	33.841	36,492	161
4	2016	Male	2288	Myroodah	197	0.341 ± 0.442	20.171	33.964	36,046	161
5	2016	Male	2285	Myroodah	197	0.371 ± 0.475	20.040	33.381	25,151	95
6	2017	Male	1296	Money	184	0.325 ± 0.507	20.003	33.506	35,941	157
7	2017	Male	1313	Money	184	0.287 ± 0.408	19.631	31.876	31,340	173
8	2017	Male	2230	Myroodah	182	0.403 ± 0.417	20.368	33.938	61,391	187
9	2017	*NA*	2224	Myroodah	183	0.354 ± 0.418	20.318	33.472	56,350	162
10	2017	Female	2645	Myroodah	183	0.448 ± 0.470	19.422	33.466	48.476	155
11	2018	Male	1598	Money	226	0.329 ± 0.473	19.272	34.506	39,802	139
12	2018	Male	1538	Money	226	0.286 ± 0.332	19.351	33.108	52,987	56
13	2018	Male	1565	Money	226	0.226 ± 0.318	19.234	34.058	55,058	102
14	2019	Male	1714	Money	209	0.238 ± 0.433	20.486	34.013	20,092	147
15	2019	*NA*	1773	Money	209	0.328 ± 0.459	20.422	33.472	19,149	156
16	2019	*NA*	1483	Money	211	0.413 ± 0.569	20.209	33.860	18,625	154
17	2019	*NA*	1894	Money	210	0.462 ± 0.579	20.503	33.133	20,718	155
18	2019	Male	1733	Myroodah	207	0.731 ± 0.944	21.257	33.491	27,104	139
19	2019	Female	1823	Myroodah	207	0.351 ± 0.415	21.204	33.617	21,382	141

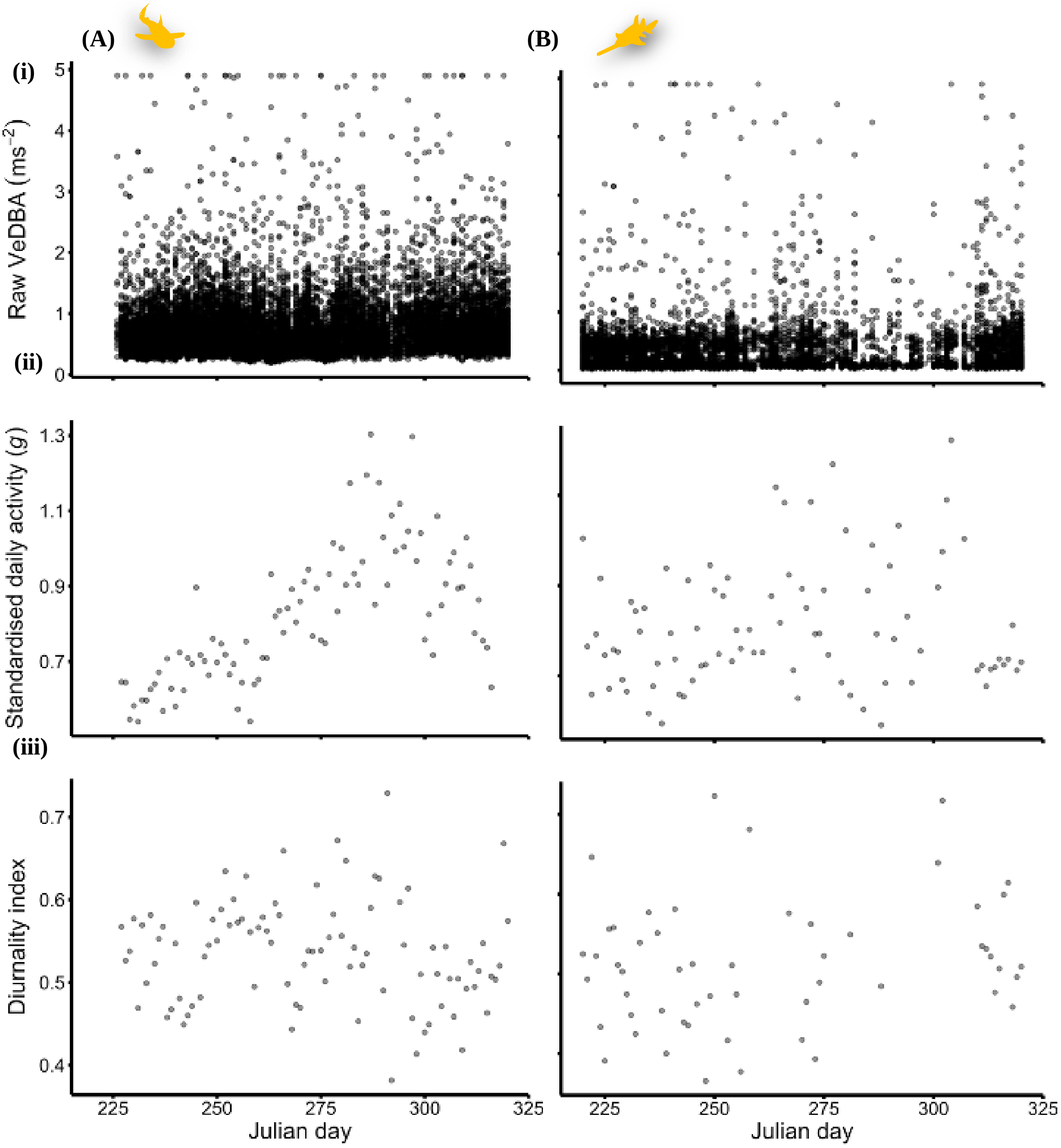

Figure 3.1: Scatterplots of (i) raw vectoral dynamic body acceleration (VeDBA) values, (ii) standardised daily activity and (iii) diurnality index for (A) a single bull shark (*C. leucas*) (ID=3) and (B) a single largetooth sawfish (*P. pristis*) (ID=16) across a period of 100 Julian days from the Fitzroy River, north-western Australia. Scatterplot demonstrates data processing that occurred prior to statistical analyses. The same principles apply to the dawn and dusk crepuscularity indices. (ii) standardised daily activity and (iii) diurnality index were used to calculated ICC for use in analysis. Raw VeDBA values were additionally converted into 0s (inactive) and 1s (active) prior to processing into standardised daily activity and diurnality index using histogram segregation demonstrated in Appendix 2.

3.2 Repeatability of activity

Between-individual variation

The intraclass correlation coefficient (ICC) of standardised daily activity increased with increasing Julian day for largetooth sawfish ($p < 0.01$) but did not significantly change with Julian day for bull sharks ($p > 0.05$) (Figure 3.2 A). An increase in ICC means that activity became less variable among individuals across the study period (i.e., behaviours are becoming more repeatable). The ICC of diurnality decreased with increasing Julian day for largetooth sawfish ($p < 0.01$) and did not significantly change with Julian day for bull sharks ($p > 0.05$) (Figure 3.2 B). A decrease in ICC for diurnality meant that individuals were becoming more active at similar times, resulting in behaviours becoming less repeatable. The ICC of both dawn and dusk crepuscularity indices for the largetooth sawfish and bull shark did not significantly change ($p > 0.05$). Overall, the mean ICC for standardised daily activity was 0.720 for bull sharks and 0.555 for largetooth sawfish. ICC was more variable in bull sharks, with ICC of standardised daily activity ranging from 0.037 to 0.953 and 0.106 to 0.871 for bull sharks and sawfish respectively (Figure 3.2 A). Overall, the mean ICC for diurnality was 0.273 for bull sharks and 0.419 for largetooth sawfish. ICC varied to a similar degree in both species; ICC range was 0.013 to 0.801 for bull sharks and 0.007 to 0.758 for sawfish (Figure 3.2 B). The mean ICC for dawn and dusk crepuscularity indices was 0.185 and 0.184, respectively, for sawfish and 0.421 and 0.311, respectively, for bull sharks (Figure 3.3). Sawfish had a greater range in the ICC than bull sharks for both crepuscularity indices. Bull shark ICC ranged from 0.013 to 0.611 and 0.037 to 0.402 for dawn and dusk crepuscularity, respectively (Figure 3.3). Sawfish ICC ranged from 0.005 to 0.788 and 0.001 to 0.779 for dawn and dusk crepuscularity indices, respectively (Figure 3.3). Top models were those models that accounted for Julian day as a variable for both species.

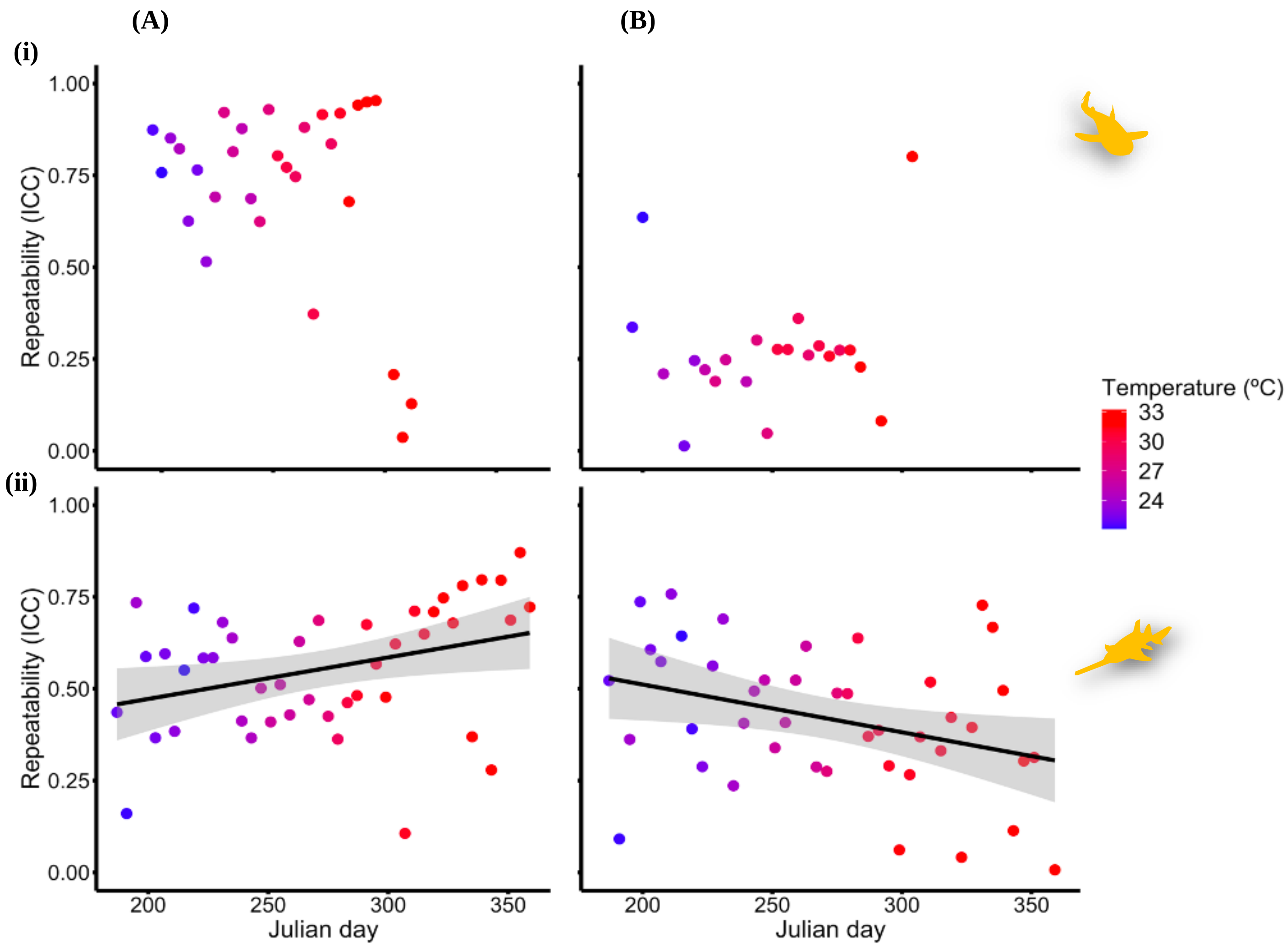

Figure 3.2: (A) Standardised daily activity and (B) diurnality index of (i) bull sharks (*C. leucas*) (n=11) and (ii) largetooth sawfish (*P. pristis*) (n=19) in the Fitzroy River, north-western Australia, 2015 to 2019. Intraclass correlation coefficient (ICC) calculated for standardised daily activity and diurnality index across Julian day with 95% confidence interval (shaded area). Points are coloured by mean daily temperature experienced by individuals. Lines are displayed for where relationships between ICC and Julian day were significant using an F-test.

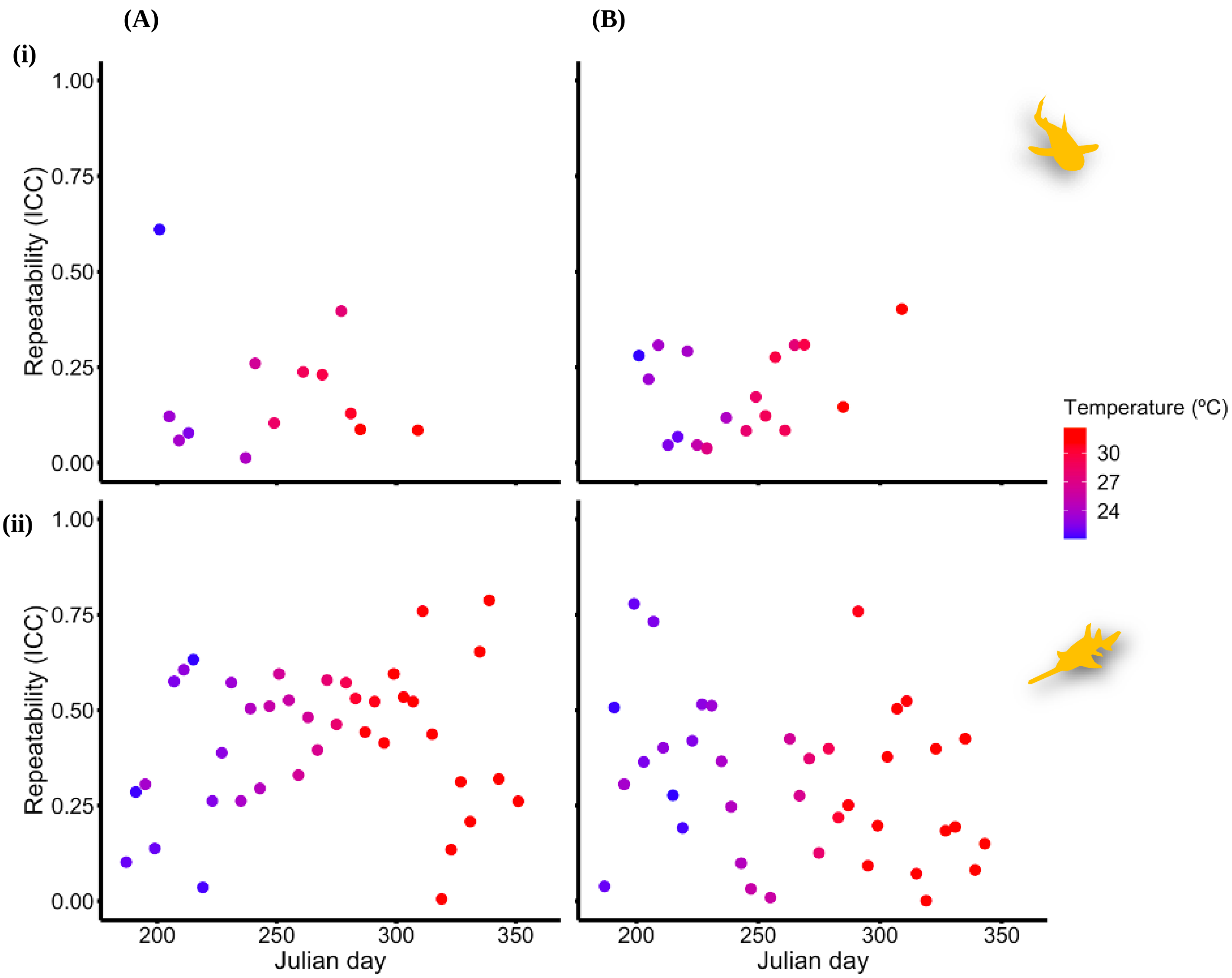

Figure 3.3: (A) Dawn and (B) dusk crepuscularity indices of (i) bull shark (*C. leucas*) (n=11) and (ii) largetooth sawfish (*P. pristis*) (n=19) in the Fitzroy River, north-western Australia, 2015 to 2019. Intraclass correlation coefficient (ICC) calculated for standardised daily activity and diurnality index across Julian day. Points are coloured by mean daily temperature experienced by individuals.

Within-individual variation

Within-individual variation (i.e., consistency) was calculated for nine bull sharks and 15 sawfish. Individual ID was the only covariate included in all models exploring drivers of within-individual variation with no environmental covariates included in top models (Table 3.2). The random effect of individual ID accounted for 31.0%, 43.1%, 21.4%, and 32.9% of the variation in bull shark standardised daily activity, diurnality, dawn crepuscularity and dusk crepuscularity, respectively. Individual ID accounted for 2.0%, 34.2%, 23.6%, and 33.8% of the variation in the dataset for sawfish standardised daily activity, diurnality index, dawn crepuscularity index and dusk crepuscularity index, respectively.

Table 3.2: Model selection table for bull shark (*C. leucas*) and largetooth sawfish (*P. pristis*) standardised daily activity, diurnality index, dawn crepuscularity index and dusk crepuscularity index linear mixed models. Selection table includes model formula and model selection criteria of AICc and delta AICc, loglikelihood, and Akaike weight of the top four model iterations for each linear mixed model. Top model selected through parsimony.

Model term	**AICc**	**Δ AICc**	**Loglikelihood**	**Akaike weight**
Bull shark (*C. leucas*) standardised daily activity				
*****Consistency ~ (1 | ID)***	***-626.1***	***0.00***	***316.098***	***0.945***
Consistency ~ Year + (1 | ID)	-619.4	6.63	313.828	0.034
Consistency ~ Sex + (1 | ID)	-617.7	8.34	312.975	0.015
Consistency ~ Location + (1 | ID)	-615.2	10.90	312.751	0.004
Bull shark (*C. leucas*) diurnality index				
*****Consistency ~ (1 | ID)***	***-633.4***	***0.00***	***319.784***	***0.894***
Consistency ~ Year + (1 | ID)	-627.5	5.94	317.859	0.046
Consistency ~ Sex + (1 | ID)	-627.3	6.13	317.767	0.042
Consistency ~ Mean temperature + (1 | ID)	-624.9	8.56	316.550	0.012
Bull shark (*C. leucas*) dawn crepuscularity index				
*****Consistency ~ (1 | ID)***	***-889.9***	***0.00***	***448.010***	***0.971***
Consistency ~ Year + (1 | ID)	-881.5	8.40	444.857	0.015
Consistency ~ Sex + (1 | ID)	-881.3	8.61	444.753	0.013
Consistency ~ Location + (1 | ID)	-875.4	14.51	442.862	0.001
Bull shark (*C. leucas*) dusk crepuscularity index				
*****Consistency ~ (1 | ID)***	***-861.3***	***0.00***	***433.706***	***0.953***
Consistency ~ Year + (1 | ID)	-854.3	6.96	431.274	0.029
Consistency ~ Sex + (1 | ID)	-853.1	8.21	430.647	0.016
Consistency ~ Location + (1 | ID)	-846.6	14.67	428.477	0.001
Largetooth sawfish (*P. pristis*) standardised daily activity				
*****Consistency ~ (1 | ID)***	***-1415.0***	***0.00***	***710.524***	***0.991***
Consistency ~ Sex + (1 | ID)	-1404.7	10.34	706.372	0.006
Consistency ~ Location + (1 | ID)	-1401.9	13.10	706.013	0.001
Consistency ~ Mean temperature + (1 | ID)	-1401.8	13.21	704.939	0.001
Largetooth sawfish (*P. pristis*) diurnality index				
*****Consistency ~ (1 | ID)***	***-1171.5***	***0.00***	***588.797***	***0.973***
Consistency ~ Sex + (1 | ID)	-1163.8	7.79	585.922	0.020
Consistency ~ Lunar phase + (1 | ID)	-1160.3	11.20	586.265	0.004
Consistency ~ Location + (1 | ID)	-1159.6	11.99	584.843	0.002
Largetooth sawfish (*P. pristis*) dawn crepuscularity index				
*****Consistency ~ (1 | ID)***	***-1403.0***	***0.00***	***704.538***	***0.988***
Consistency ~ Sex + (1 | ID)	-1393.9	9.14	700.986	0.010
Consistency ~ Mean temperature + (1 | ID)	-1389.0	13.99	698.564	0.001
Consistency ~ Location + (1 | ID)	-1388.2	14.78	699.193	0.001
Largetooth sawfish (*P. pristis*) dusk crepuscularity index				
*****Consistency ~ (1 | ID)***	***-1259.5***	***0.00***	***632.803***	***0.957***
Consistency ~ Sex + (1 | ID)	-1252.2	7.32	630.163	0.025
Consistency ~ Mean temperature + (1 | ID)	-1251.1	8.41	629.620	0.014
Consistency ~ Location + (1 | ID)	-1248.2	11.30	629.196	0.003

** top model for selection

4 Discussion

This study is the first to demonstrate telemetry-derived acceleration data as a method to assess long-term repeatability of behaviour in free-ranging animals and examine the concurrent impact of biotic and environmental drivers on personality. These findings confirm that, in some cases, individual personality is apparent in free ranging animals and that differences among individuals change throughout the year in response to environmental and physiological conditions. Repeatability of behaviour was exhibited differently in two species with contrasting lifestyles; the pelagic, fast-paced lifestyle of the bull shark compared to the demersal, slow-paced lifestyle of the largetooth sawfish. This difference was likely a result of their divergent lifestyles.

4.1 Acoustic telemetry as a means to determine repeatability of behaviour

Overall, we were able to calculate Intraclass correlation coefficients (ICC), a measure of the degree of correlation between repeated measurements of a class of data (Liljequist et al. 2019), for naturally occurring activity in two free-ranging vertebrates and the ensuing data are comparable with those gathered from experiments under controlled conditions. Since the ICC is thought to be a measurement of personality (Bell et al. 2009; Hayes et al. 1997), this suggests that the activity of free-ranging animals is a viable option to assess repeatability of behaviour.

The ICC has been used to describe animal personality in a range of taxa, including apes (Garai et al. 2016; Massen et al. 2013), amphibians (Michelangeli et al. 2016), birds (Holtmann et al. 2017) and fish (Fürtbauer et al. 2015). Variation in ICC reports a change to the degree of prevalence of personality. Low ICC indicate low repeatability and low prevalence of personality whereas high ICC indicate high repeatability and prevalence of personality (e.g., Konečná et al. 2008). In some cases, very low ICC values (i.e., < 0.2) are thought to demonstrate non-significance for trends in repeatability and personality (e.g., Fürtbauer et al. 2015), though large ranges are not uncommon in captive animals (see Tetley et al. 2012). Here, ICC is used to support the hypothesis that free-ranging elasmobranchs display personality. ICC values, at their highest, were 0.953 for bull sharks and 0.871 for largetooth sawfish. These values are seen as 'remarkably high' (Massen et al. 2013), twice the mean ICC found for repeatability of behaviour in both captive and captured wild bird populations (ICC=0.410) (Holtmann et al. 2017) and almost double those found in a skink trapping study (ICC range: 0.32–0.49) (Michelangeli et al. 2016). This provides additional evidence to support that both bull sharks and largetooth sawfish exhibit personality, and activity measured through acoustic telemetry to be a viable means of quantifying repeatability and personality.

The disconnected pools that sawfish and bull sharks occur in during the dry-season alongside high receiver coverage in those pools resulted in a large data-set with few to no gaps, which are often common in acoustic telemetry studies. The significant data volume is the main reason why I was able to perform detailed analysis of repeatability of behaviour, however this may not be the case in other studies as detection probabilities in this study were exceptionally high compared to other studies, primarily because individual animals are less geographically restricted in their movement (e.g., Nichols et al. 2000; Szesciorka et al. 2020; Wilson et al. 2006b). Additionally, even for species that establish home-ranges, these can greatly vary in size (see Kramer et al. 1999), with some taking up large areas (> 1000 m) of marine coastal environments. Under these situations, it would not be economically feasible to deploy sufficient numbers of acoustic receivers to ensure similar volumes of data to those that were collected for this study. For example, white shark (*Carcharodon carcharias*) movements tracked using acoustic telemetry detected 182,000 transmissions from 43 tagged sharks across 287 receivers and 7 years of study (Bruce et al. 2019). By comparison, 56,350 transmissions were recorded from one sawfish across 162 days in this study, further demonstrating how the study location allows for greater detections and sample size. However, telemetry is a rapidly evolving field and other tracking methods may be used to obtain similar results. Satellite telemetry (i.e., tracking animals through satellite) may present a future option that could be used to collect data on diving and activity patterns of marine mammals, sharks, and turtles (e.g., Godley et al. 2002). Additionally, using a combination of satellite and acoustic tags may prove beneficial in certain environments and allow for the collection of fine- and broad-scale movements (Crossin et al. 2017; Heupel et al. 2006). The field of telemetry, whether acoustic or satellite, provides an opportunity for overcoming the logistical issues associated with controlled studies on animal behaviour and, despite their limitations, still offer the most widely applicable method for studying personality in the wild.

Prior to statistical analyses, bull shark data were not converted into active or inactive states due to the difficulties in distinguishing between activity levels associated with the species' relatively active lifestyle. Although this was appropriate for the analysis of repeatability of activity, it is possible that the different treatment of sawfish and bull shark data is rendering comparisons between the species problematic. Not separating bull shark activity states could overestimate true activity; bull sharks may be seen to be in an 'active' state even when they are being proportionally less active and undertaking a form of 'rest'. This may have consequences for interpretation of results as there may be more overlap in activity patterns for bull sharks, potentially limiting the ability to detect signal in the data. Although it may not overcome these issues, future studies may consider hidden Markov models (HMMs) in allowing for better intraspecific comparison of bull shark behaviour (e.g., Byrnes et al. 2021).

HMMs, or doubly-embedded stochastic processes, are used to describe observable events that result from internal factors that are difficult to observe (e.g., activity states that result from predominately active data) (Yoon 2009). Other similar unsupervised data clustering methods, such as k-means (Zhang et al. 2015) could also be appropriate for distinguishing activity states, allowing more accurate comparison of repeatability of behaviour. However, analysis on raw sawfish activity data (i.e., prior to being converted into activity states) did not differ in trends in repeatability of behaviour to that of data converted into activity states (unpublished data). As trends in repeatability of behaviour were similar for both raw and converted sawfish data it is unlikely that there will be a change in these trends for bull sharks and, therefore, methods were not modified for this research.

4.2 Environmental determinants of repeatability

Despite the known importance of sexual differences (Garai et al. 2016; Holtmann et al. 2017; Schuett et al. 2009), body size (Biro et al. 2008) and metabolism (Careau et al. 2008) in driving behaviour, how individuals respond to and cope with environmental challenges in this system appears to be mostly individualistic. ICC varied across the study period, indicating a change in the prevalence of personality in behavioural responses. ICC ranged from very low (0.037, 0.106) to very high (0.953, 0.871) for both bull sharks and largetooth sawfish, respectively, across the study period. Interestingly, the contrasting lifestyle of the two species revealed different results, with only one species showing a temporal change in ICC: the largetooth sawfish. The pelagic, ram ventilating bull shark did not show significant trends in repeatability of any behavioural traits (i.e., ICC in daily activity or activity rhythm). This might indicate that although bull sharks exhibit personality, under the prevailing conditions, the environmental change during the study were either insufficient for individual bull sharks to differentially alter their behaviour, or that ecological constraints prevented individuals from differential expression of behaviour.

One explanation for the lack of seasonal changes in the prevalence of personality of bull sharks is the higher metabolism that is characteristic of species that rely on ram ventilation (Carlson et al. 2004). Standard metabolic rate of largetooth sawfish and bull sharks in the Fitzroy River are between 63-187 mg O_2 $kg^{-0.86}$ hr^{-1} and 187-506 mg O_2 $kg^{-0.86}$ hr^{-1} respectively (Lear et al. 2020). As bull sharks have significantly greater mass specific metabolic rates than sawfish, they suffer from an approximate doubling of mass loss during the resource limited dry season (Lear et al. 2020). This suggests that bull sharks face considerably greater physiological stress at the time of our study which may potentially hamper the ability of individuals to mount a different behavioural response to the environmental changes they encounter (see Ng et al. 2017).

The differential stress experienced by the two species studied here may also represent a causative factor in their ability to respond to environmental change. Specifically, largetooth sawfish have considerably greater control over their activity-related energy expenditure since they are able to rest motionless on the riverbed. This resting behaviour may also allow for greater access of microclimates, which may be constrained to relatively small areas that are difficult to exploit in a species unable to rest, thus offering another means of controlling metabolism that is not afforded to bull sharks in the same manner (see Johnson 1975). Indeed, the reduction in repeatability of the diurnality index in sawfish with increasing temperatures indicates that individual specialisation reduces with increasing temperatures (i.e., individual sawfish activity patterns are becoming increasingly alike). One explanation for this phenomenon is that increasing temperatures result in a decline of the spatio-temporal extent of suitable microclimates, forcing animals to adopt similar activity patterns. During our study period, the Fitzroy River stratifies most days, with deeper depths consistently 2-3°C colder than surface waters during the hottest part of the day. Since surface water temperatures in the late dry season exceed the thermal optimum for sawfish (Lear et al. 2020), sawfish may increasingly be forced to adopt an activity rhythm that avoids the warm surface waters where these animals are mostly thought to forage and rest in cool deep waters during the day (Whitty et al. 2017). Such "thermal refuging" is a process by which individuals alter the timing of their important activities, usually by avoiding undertaking them during the hottest part of the day (Buchholz et al. 2019). This diel activity pattern may be less pronounced, and less beneficial to individuals, during the early dry season when temperatures are not exceeding thermal optima and are not approaching critical temperatures, instead allowing individuals to partition the diel cycle. In addition to the hypothesis that increasing temperatures may result in a temporal redistribution of activity, it is also conceivable that increasing temperatures invariably result in greater overlap of the timing of activity simply as a result of individuals increasing time engaged in active behaviours to compensate for their greater metabolism (Gleiss et al. 2017; see also Gannon et al. 2014; Payne et al. 2016).

The approximate doubling of metabolic rates and associated energy requirements of individual sawfish and bull sharks, and other ectothermic predators (e.g., the estuarine crocodile, *Crocodylus porosus* and freshwater crocodile *Crocodylus johnsoni* (Lear et al. 2019)), is also expected to cause an increase in inter- and intra-specific competition for resources in this system. The Fitzroy River, like all dryland rivers, is characterised by very low productivity in the dry season, compared to the wet season, thus competition may naturally increase as a combined result of decreasing resource supply and increasing energy demand.

Individual specialisation may help to mitigate this increased competition; individuals may selectively perform activities (i.e., foraging) at different times, reducing the probability of encountering conspecifics (temporal partitioning). Moreover, if individuals are foraging at different times, they may also invariably exploit different prey, as the availability of specific prey will also vary a function of time of day. The decreasing ICC of the diurnality index across the study period suggests that early in the year, animals temporally partition their activity and behaviour, but as the year progresses increasingly display temporal overlap. This apparent increase in competition is potentially mitigated through behavioural specialisation. An increase in ICC for standardised daily activity may indicate that personality traits related to the level of activity are becoming more prevalent with increasing energy demands and competition. Different individuals may exhibit different strategies to mitigate competition, with some personality types being beneficial under certain environmental regimes, and others being detrimental. For instance, bold and exploratory individuals may be able to mitigate this competition by increasing activity and foraging behaviour, potentially exploiting risky resources, while shy and less exploratory individuals may restrict their activity and foraging behaviour to reduce their need to exploit risky resources (Dhellemmes et al. 2020; Moiron et al. 2020).

4.3 Conclusion and wider implications

The results from this thesis demonstrate that animal personality (i.e., repeatability of behaviour) exists in the field and, importantly, provides the first account that personality can be measured through acoustic telemetry. This study demonstrates a new avenue of data collection for personality research and the constantly evolving technology associated with biologging may allow personality research to move from the laboratory to the field, allowing greater understanding of the ecological relevance of personality. Repeatability of behaviour is variable in the field environment, likely a response to environmental changes and associated physiological responses. Specifically, an increase in temperature, metabolism, and energetic demand in a resource-limited environment places competition pressures on individuals. Responses to these changes appear to be highly individualistic, demonstrated through both ICC and consistency model selection. The changes that occur in the Fitzroy River basin are compounded by increases in evaporation and lack of precipitation across the June to December study period. Continuous drying of the pools through the season leaves less volume of water to be heated by sunlight, causing rapid increases in water temperatures, and as such metabolic rates. Simultaneously, decreasing forage supply exacerbates difficulties in meeting these increased metabolic demands. Further studies in this area may help realise how similar species, elasmobranchs and other aquatic ectotherms may respond to climate change and associated environmental changes. Pelagic, generally active species that have similar lifestyles and metabolic demands to bull sharks may be at higher risk to environmental changes as they may have reduced capacity for behavioural flexibility, as demonstrated here. Subsequently, under the extreme conditions of the Fitzroy River the slow-paced lifestyle of the largetooth sawfish may better equip it for responding to environmental challenges. As such, it has been demonstrated that it is important to understand the interrelated effects of personality and physiology on repeatability of behaviour and specialisation in wild animals, as these may be determining factors in how these individuals cope with change and stressors in their environment. The findings indicate that no singular aspect of personality or physiology can explain species responses to environmental change, and much more is to be explored in this area of research. Increased abilities to monitor animal behaviour and physiology through technological advances in tagging technologies make exploring personality in real-world contexts viable. In turn, this may become an important area for understanding species vulnerability in the face of climate change and the Anthropocene.

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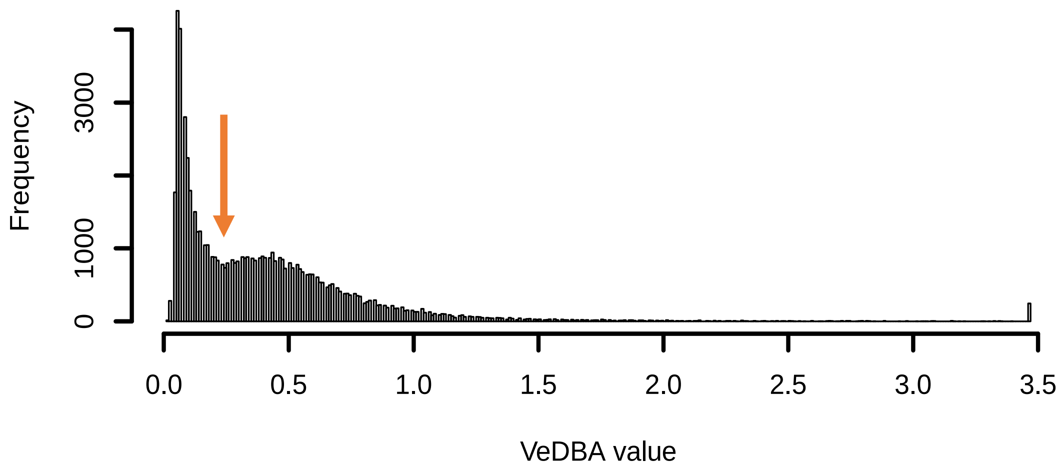
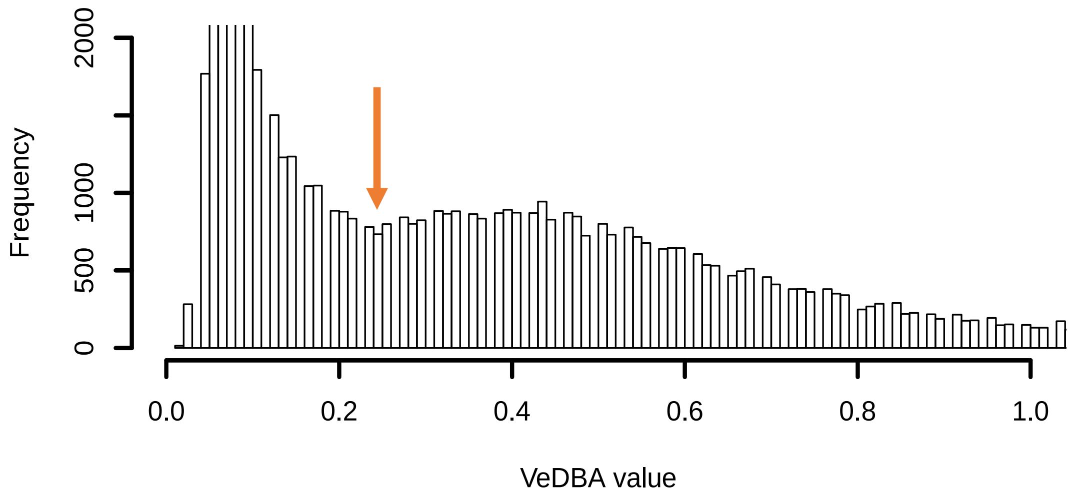
Appendices

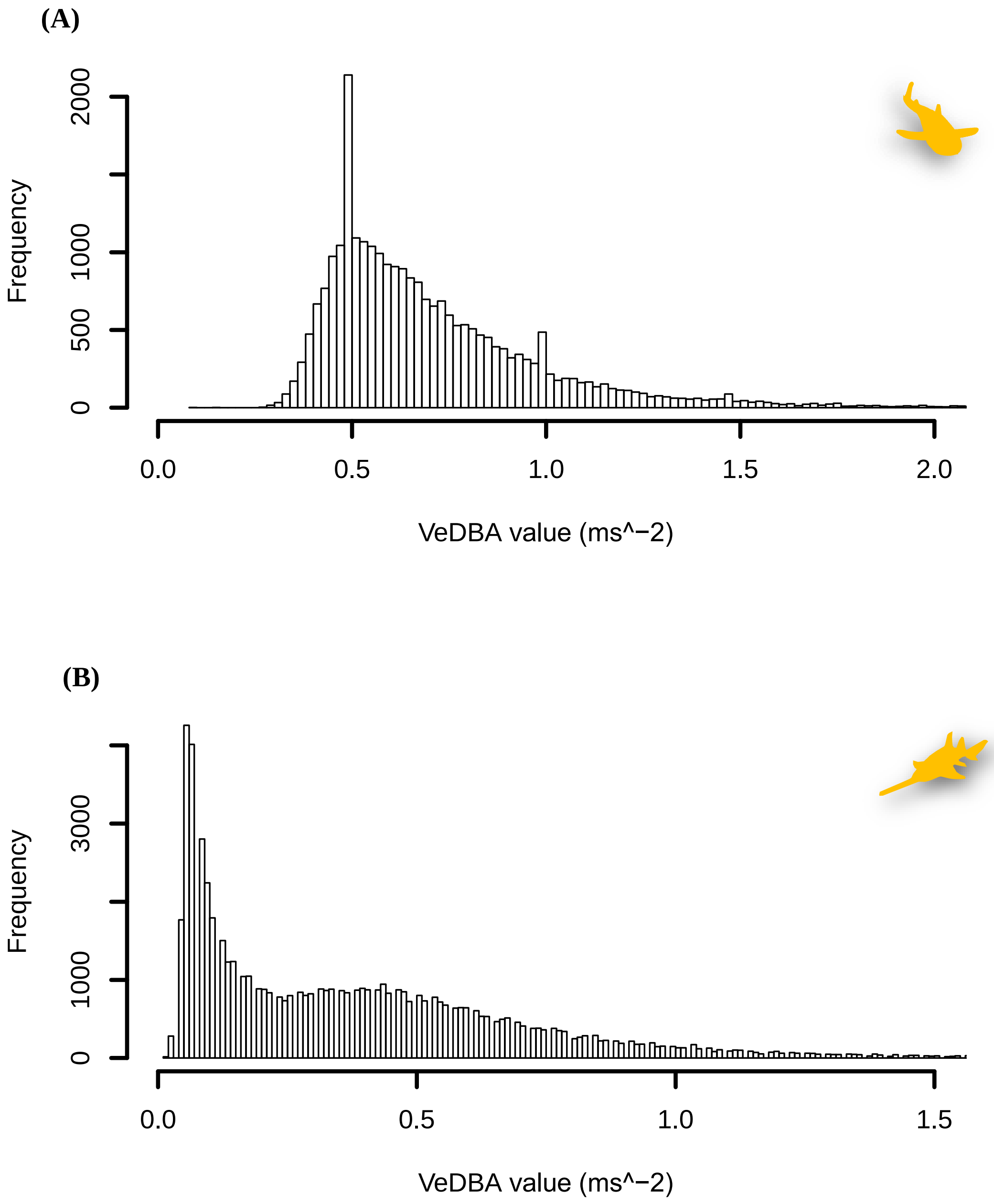
(A)



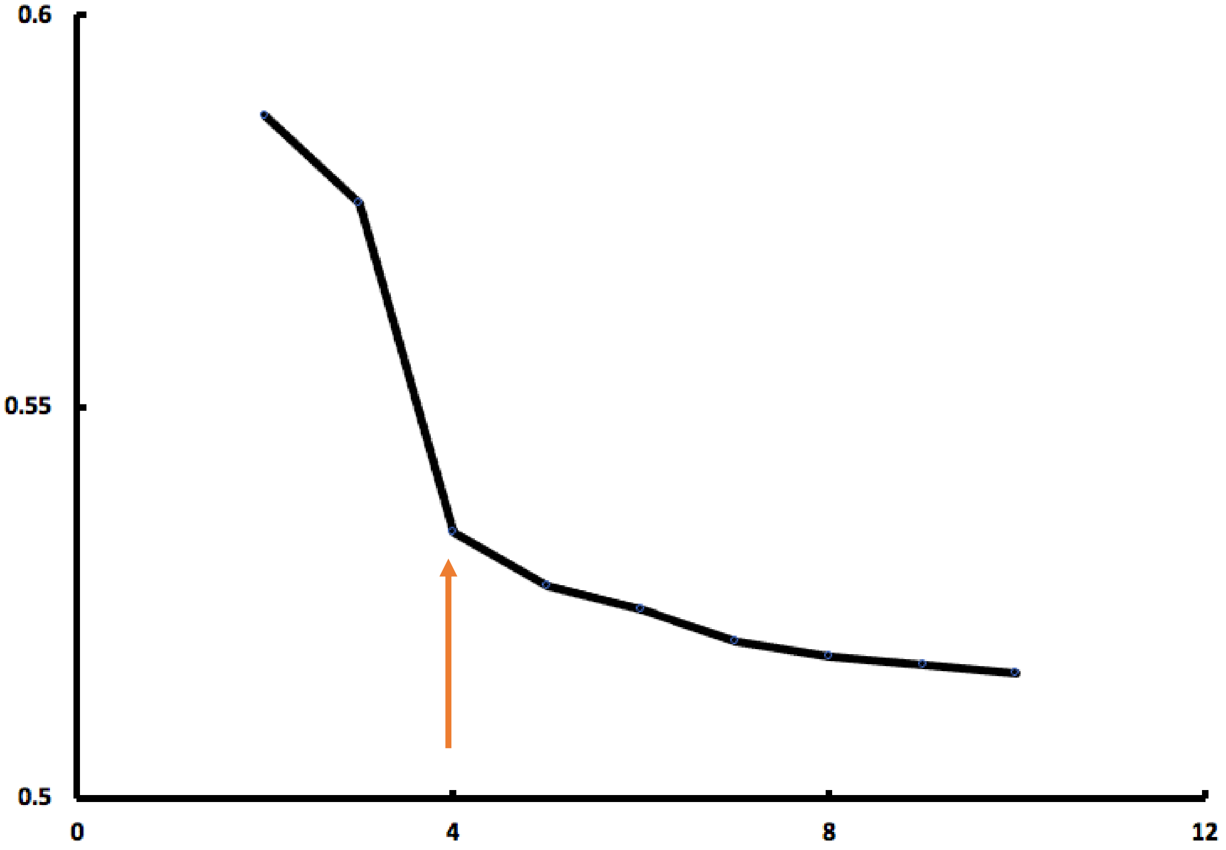
(B)



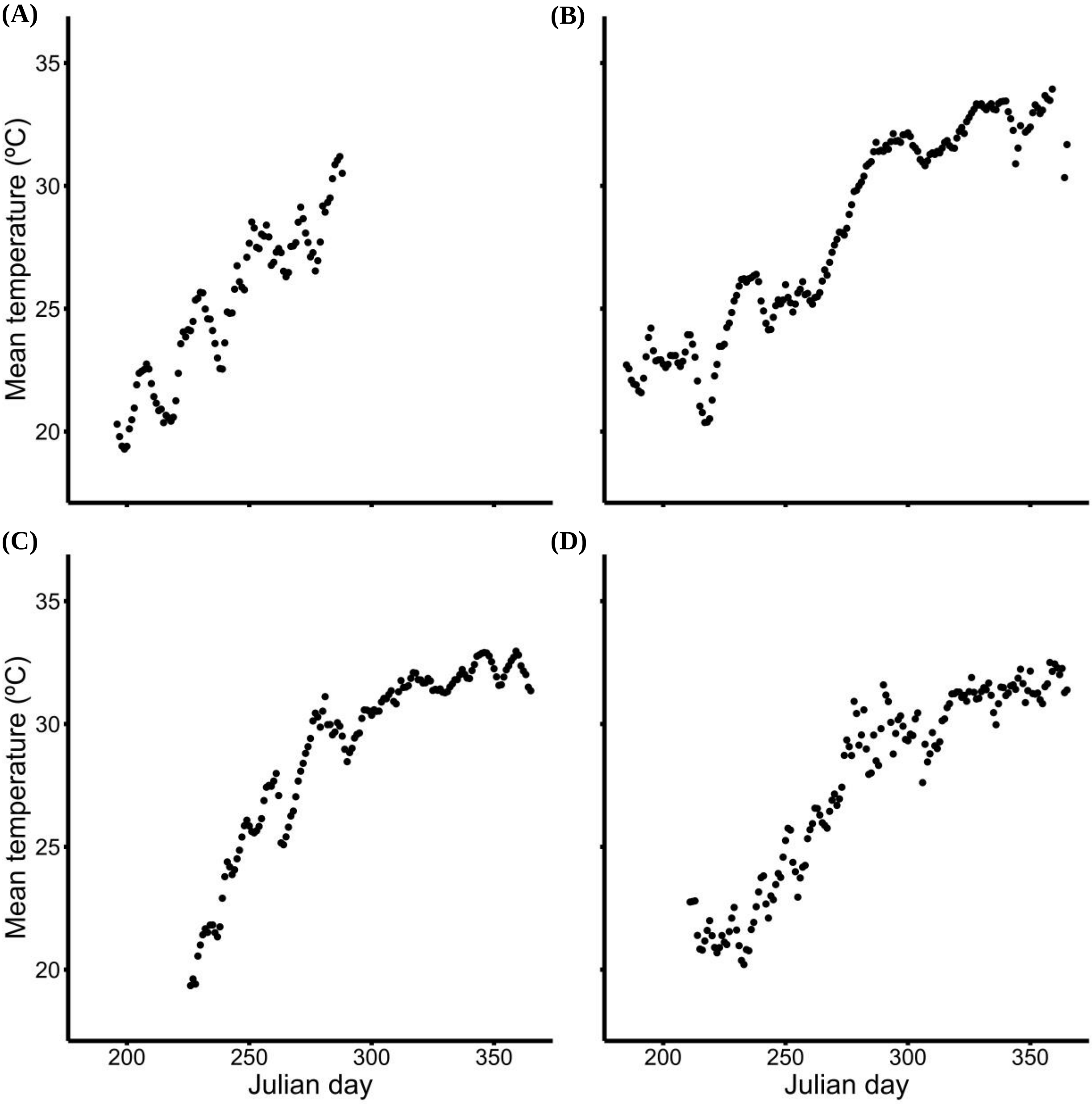
Appendix 1: Frequency distribution of raw vectoral dynamic body acceleration (VeDBA) values for (A) complete distribution of VeDBA values and (B) VeDBA values ranging from 0 to 1, with a frequency up to 2000, from a single largetooth sawfish (*P. pristis*) (ID = 8) (n = 19) from the Fitzroy River, north-western Australia. Orange arrow indicates VeDBA value with the lowest frequency immediately prior to second peak in the binomial dataset. For histogram segregation, all values before and after orange arrow were converted into 0 (inactive) and 1 (active) periods of locomotion, respectively.



Appendix 2: Frequency distribution of raw vectoral dynamic body acceleration (VeDBA) values from (A) a single bull shark (*C. leucas*) (ID = 10) (n = 11) and (B) a single largetooth sawfish (*P. pristis*) (ID = 8) (n = 19) from the Fitzroy River, north-western Australia.



Appendix 3: Elbow plot of mean largetooth sawfish (*P. pristis*) ICC from a window period of two to ten days. Orange arrow indicates point immediately following largest change in ICC (i.e., elbow). This point was the point at which the window period for further analysis was based off: four days. The same window period was true for all indices for both species between-individual and within-individual analyses.



Appendix 4: Mean daily water temperature from one individual from (A) 2016, (B) 2017, (C) 2018 and (D) 2019 from the Fitzroy River, north-western Australia.