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Faculdade de Ciências e Tecnologia

2023-2024

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Mestrado em Biologia Marinha

Trabalho efetuado sob a orientação de:

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Faculdade de Ciências e Tecnologia

2023-2024

Resumo

O desenvolvimento de dispositivos de transporte de animais (também conhecidos como bio-loggers) revolucionou o estudo de animais que podem ser difíceis de seguir visualmente, como a megafauna marinha. De facto, a utilização de bio-loggers permite-nos gerar dados sobre os movimentos livres, o comportamento e o ambiente envolvente de qualquer organismo suficientemente grande para se coloar um dispositivo de bio-logging. No entanto, embora a utilização de bio-loggers em ecologia tenha aumentado rapidamente nas últimas décadas, este aumento não foi acompanhado por um crescimento semelhante nos estudos que investigam os potenciais impactos associados à utilização de bio-loggers em animais selvagens. O nosso objetivo é, então, colmatar esta lacuna no conhecimento científico, pasando por estudar mais aprofundadamenteo impacto dos padrões de comportamento e de mergulho em tartarugas verdes juvenis (*Chelonia mydas*) em Eleuthera, nas Bahamas, através da instalação de câmaras transportadas pelos animais com gravadores incorporados de tempo e profundidade (TDR). Compreender como e durante quanto tempo, o comportamento das tartarugas verdes juvenis é afetado pela instalação de dispositivos de registo biológico permite-nos compreender melhor como interpretar os dados dos dispositivos de registo biológico para obter informações sobre os padrões de comportamento “naturais” destes animais.

Devido ao facto de as tartarugas marinhas terem pulmões e terem de estar à superfície da água para respirar, uma componente chave para compreender o seu comportamento é, então, estudar os seus padrões de mergulho. Como a duração do mergulho destes animais está intrinsecamente ligada às suas reservas de oxigénio, é de esperar que os animais que inalam mais ar para os pulmões sejam capazes de mergulhar durante mais tempo. No entanto, uma maior quantidade de ar nos pulmões aumentará também a flutuabilidade do animal. Este facto pode constituir um desafio em habitats de águas pouco profundas (uma vez que, de outro modo, a flutuabilidade do animal diminuiria com a profundidade), pois os animais com flutuabilidade positiva podem gastar mais energia para se manterem submersos e não conseguirem descansar em profundidade. Assim, é possível que as tartarugas marinhas em habitats de águas pouco profundas inspirem menos ar e, por conseguinte, tenham períodos de mergulho mais curtos do que em habitats mais profundos. Além disso, factores como os padrões de atividade e as temperaturas podem também desempenhar um papel fundamental na duração do mergulho, afectando as taxas metabólicas e o consumo de oxigénio. No entanto

até à presente data, terão efetuados poucos estudos sobre os padrões de mergulho das tartarugas marinhas em habitats de águas pouco profundas, provavelmente devido à dificuldade de identificar mergulhos individuais a partir de dados TDR nestes sistemas. Um objetivo secundário deste estudo foi a utilização de dados TDR em combinação com câmaras transportadas por animais para caraterizar os factores que determinam os padrões comportamentais de mergulho em juvenis de tartarugas verdes em sistemas de águas pouco profundas (< 5 m de profundidade).

Para tal, instalaram-se bio-registadores compostos por uma câmara e um TDR em 58 tartarugas verdes juvenis na ilha de Eleuthera, nas Bahamas. Cada instalação registada durou até 210 min (intervalo: 122 a 202,5 min) com uma duração média de filmagem de 180 ± 17 min SD. Além disso, utilizaram-se veículos aéreos não tripulados (UAVs) para gerar dados de "controlo" para 25 tartarugas que não tinham sido manipuladas previamente mas que se encontravam nos mesmos habitats. Cada registo durou cerca de 20 min (intervalo: 10 a 20 min) com uma duração média de 15 ± 2,93 min SD. Utilizaram-se as filmagens das câmaras para classificar o comportamento das tartarugas exibido em cada segundo numa de seis categorias: natação, subida à superfície, repouso, alimentação, socialização e outros comportamentos (por exemplo, cavar ou rastejar). Ao procurar padrões de comportamento ao longo do tempo, utilizaram-se os presentes dados para determinar o efeito da instalação e retenção do bio-logger. Avaliou-se ainda o efeito do tamanho do corpo nestas análises, separando as tartarugas em duas classes de tamanho com base no seu Comprimento Reto da Carapaça (SCL): "pequeno" (≤ 50 cm SCL) e "grande" (> 50 cm SCL). Para examinar os factores-chave que determinam a duração do mergulho, foram utilizados Modelos Lineares Generalizados Mistos (GLMMs) numa abordagem Bayesiana para avaliar o impacto da profundidade máxima do mergulho, da temperatura média, da duração da inalação pré-mergulho e dos padrões de atividade na duração do mergulho.

Os dados obtidos pelas câmaras revelaram que nos primeiros 30 minutos após a libertação, as tartarugas passaram entre 70 e 80% do seu tempo a nadar e tiveram uma duração média de mergulho de 45,3 ± 34,3 segundos (SD). Entre 30 e 90 minutos, a percentagem de tempo passado a nadar diminuiu à medida que o tempo de repouso e a duração dos mergulhos aumentaram até atingir um patamar estável. No entanto, os dados de "controlo" obtidos a partir do UAV indicaram que o tempo passado a nadar e as durações dos mergulhos eram mais comparáveis aos comportamentos observados imediatamente após a instalação dos bio-registadores do que após atingido o patamar. Além disso, não foram identificadas diferenças estatisticamente significativas na duração do mergulho entre as duas categorias de tamanho. A nossa hipótese é que: (1) os efeitos da instalação do bio-logger no comportamento das tartarugas são insignificantes após 90 minutos, mas os dados do UAV são tendenciosos (ou porque há uma tendência para recolher amostras de tartarugas que não estão a descansar ou porque a presença do UAV aumenta a taxa de natação das tartarugas próximas) ou (2) é necessário um período mais longo de recolha de dados (> 3h) para que os comportamentos das tartarugas regressem a níveis não manipulados, uma vez que o comportamento das tartarugas pode eventualmente regressar aos níveis relatados pelo UAV.

Este estudo registou algumas das durações médias de mergulho mais curtas observadas em tartarugas verdes juvenis. Quando comparado com outros estudos sobre tartarugas verdes que mergulham em habitats mais profundos, este facto apoia a nossa hipótese de que as tartarugas em habitats de águas pouco profundas podem limitar a quantidade de ar inalado antes de um mergulho para as ajudar a manter a flutuabilidade neutra. Este resultado foi também apoiado pelas análises de regressão gama. Contudo, apesar da profundidade máxima de mergulho neste estudo ter sido de 6,1 m, observou-se um efeito positivo significativo da profundidade na duração do mergulho. Além disso, também se observou que durante o mergulho, houve um efeito significativamente positivo da temperatura média e da duração da inspiração antes do mergulho. Relativamente à temperatura média, seria de esperar uma diminuição da duração do mergulho com temperaturas mais elevadas. Nono entanto, os nossos resultados contradizem esta previsão. Este resultado pode resultar da influência dos padrões de maré no local de estudo. As tartarugas foram libertadas, na sua maioria, durante um período em que a maré estava a baixar, resultando numa transição da água fria do oceano para a água quente do mangal, e num aumento da temperatura para as tartarugas marinhas. A descida da maré ocorreu aproximadamente uma hora após a libertação das tartarugas, altura em que as tartarugas tiveram tempo suficiente para relaxar, e a duração do mergulho aumentou, apesar do aumento da temperatura. Os nossos resultados releveram também que as durações de mergulho mais curtas estão associadas a uma maior probabilidade de comportamento ativo e a uma menor probabilidade de comportamento de repouso. Taxas de atividade mais elevadas aumentam provavelmente o consumo de oxigénio, diminuindo a duração dos mergulhos. Em suma, pode concluir-se que : (1) as curtas durações de mergulho observadas em sistemas de águas pouco profundas podem estar associadas à manutenção de flutuabilidade neutra ou negativa, (2) as tartarugas marinhas podem prolongar a duração do mergulho inalando várias vezes antes de um mergulho, e (3) os padrões de atividade são um fator significativo que determina a duração do mergulho em sistemas de águas pouco profundas.

Abstract

Animal-borne devices (= bio-loggers) have revolutionized marine megafauna research. Nevertheless, there is limited data on how bio-logger attachment and handling stress affect animals. This study used animal-borne cameras with time-depth recorders to examine short-term diving behavior (< 210 min) and the factors driving dive duration in juvenile green turtles (*Chelonia mydas*) in understudied shallow water habitats (< 5 m depth) in The Bahamas. We compared the behavior of 58 turtles with bio-loggers to 25 non-handled turtles observed by Unoccupied Aerial Vehicles (UAVs), which do not cause panic in turtles. After release, turtles spent 70-80% of their time swimming with a mean dive duration of 45.3 ± 34.3 seconds (SD). Over 90 min, dive duration increased while swimming time decreased until stabilizing. However, the UAV data was similar to turtle behavior immediately after bio-logger deployment, suggesting that bio-loggers and handling stress influence diving behavior for at least 90 min. Afterward, the effect of bio-loggers either: (1) has a small effect and UAVs may produce biased data on "natural" turtle behavior or (2) a longer period of data collection (> 3h) is necessary for turtles to return to non-handled behaviors. This study recorded some of the shortest mean dive durations observed for juvenile green turtles (66.43 ± 75.85 seconds SD). Maximum dive depth, breath duration, and mean temperature exhibited a statistically significant positive effect on dive duration. Longer breath duration provided more oxygen, allowing longer and deeper dives. Tidal patterns increased temperature when the turtles were already relaxed, which prolonged dive duration despite typically raising metabolic rates. The likelihood of active behavior decreased throughout the dive duration while resting increased, reflecting oxygen use: active behaviors require more oxygen, shortening dives, while resting allows longer dives. In conclusion, juvenile green turtles in shallow waters do not perform long dives, and (2) dive duration is influenced by breath duration and activity patterns.

KEYWORDS

Animal-borne cameras, UAVs, bio-loggers, handling stress, dive duration, sea turtles

Acknowledgments

I would like to extend my sincere thanks to my master's thesis supervisor, Dr. Nathan J. Robinson, for giving me the opportunity to participate in this project and learn about the world of sea turtles, for his patience and constant feedback during this year, but also for helping me in my career as a scientist.

I also would like to thank Dr. Damianos Chatzievangelou for his patience in teaching me all the statistics and modeling carried out (with my thousand questions), and for constantly guiding me together with Dr. Nathan J. Robinson. Thank you both for trusting me to do this incredible research project.

I would also like to thank Sophie K. Mills, who carried out the first labeling of the video data at her time, as well as José M. Reyes-González, for helping us with his experience in treating models of animal behavior.

I could not have done this without my family and friends. Thank you for your constant encouragement and support in the most difficult moments.

And thank you, Daniela, for your endless support. We had such a great time working together side by side (literally). This experience would not have been the same without you. Adoro-te, minha amiga

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List of abbreviations

BF	Bayes Factors
CCL	Curve Carapace Length
CCW	Curve Carapace Width
CI	Credible Intervals
CL	Carapace Length
ELPD	Expected Log Predicted Density
GLMM	Generalized Linear Mixed Models
H_0	Null Hypothesis
H_1	Alternative Hypothesis
H_{-1}	Complementary Alternative Hypothesis
HDI	Highest Density Interval
LOOIC	Leave-One-Out Information Criterion
MAP	Maximum A Posteriori probability estimate
MCMC	Markov Chain Monte Carlo
PSIS	Pareto-Smoothed Importance Sampling
ROPE	Region of Practical Equivalence
SCL	Straight Carapace Length
SCW	Straight Carapace Width
SD	Standard Deviation
SE	Standard Error
TDR	Time-depth recorder
TurtleCam	Animal-borne cameras
UAV	Unoccupied Aerial Vehicle

CHAPTER 1: Introduction

1. Innovations in monitoring sea turtle behavior

Understanding animal behavior is one of the key pillars of ecology, and it may help guide conservation efforts as it focuses on the personalities of individual animals and how they react to changes in their surroundings (Bryant, 1989; Dingemanse et al., 2010). However, marine megafauna such as sea turtles are challenging to observe *in situ* as they spend most of their time underwater (Hochscheid, 2014; Hounslow et al., 2022). As such, researchers frequently use animal-borne devices (= bio-loggers) with the capacity to generate data on the host animal (e.g., behavior, swim speed, etc.) and/or its immediate surroundings (e.g., temperature, depth, etc.) (Rutz & Hays, 2009; Hochscheid, 2014). Bio-loggers are different from telemetry devices, which can collect and transmit behavioral and environmental data remotely (Goodwin et al., 2008). The use of animal-borne devices has revolutionized the field of behavioral ecology by enhancing our understanding of the physiology, behavior, and ecology of certain marine megafauna (Kooyman, 2004; Ropert-Coudert et al., 2009).

Deploying bio-logging devices inherently requires physical interaction with the target animal. This interaction might include both the device's deployment and the animal's restraint during this process. This process may present an injury risk to both the animals and the researchers (Harcourt et al., 2010). Moreover, any instance where a wild animal needs to be handled may provoke a stress response that could impact their behavior after release (Flower et al., 2015). In fact, some studies suggest that sea turtles presented higher levels of corticosterone a few hours after being captured (Gregory et al., 1996), which is a common indicator of stress in wild animals (Baker et al., 2013). Thus, when deploying bio-logging devices the handling time should be minimized to reduce the stress experienced by the turtles, thereby allowing a more accurate representation of their behavior and ensuring a more ethical methodology (Hochscheid, 2014). Furthermore, for instance in emperor penguins, some bio-logging devices are attached to their back feathers using glue, which may cause an excessive feather break (Houstin et al., 2021). In other cases, for example in sea turtles, bio-logging devices are attached by drilling fixture holes through the marginal rim of the carapace (e.g., Hill et al., 2017) or with suction cups (e.g., Hounslow et al., 2022). Besides handling stress, an animal’s behavior may also be impacted by the physical presence of the bio-logging device. In marine environments, because of the effect of buoyancy, the impact of bio-logging devices' mass has less of an impact on the organisms than the total increase in drag (Jones et al., 2011). For instance, dorsal fin attachment to small cetaceans and tag antennas in penguins increase drag up to 70% in both cases (Hanson, 2001; Wilson et al., 2004), whereas satellite tags increased drag up to 10-14% in pinnipeds (Hazekamp et al., 2010). The increase in drag may correspond to an increase in the animal's power output or may impact the animal's ability to swim (Jones et al., 2013), which could consequently influence its behavioral patterns. Therefore, studies should consider how this increase in drag impacts the target organism. Although it is challenging to know whether an animal is aware of a bio-logging device attached to it, for example, sea turtles have been observed to frequently scratch their shells against objects, maybe as a means of cleaning their shells (Harvey-Carroll et al., 2024). Therefore, a turtle may scratch its shell more frequently if it feels the bio-logger's presence. It is crucial to determine the extent of the impact of handling stress and bio-logging attachment on the diving behavior of the target organism, as this will facilitate the interpretation of the data obtained and provide insight into the "natural" behavioral patterns of these animals. Nevertheless, to date, only one study (Thomson & Heithaus, 2014) has made an effort to determine how turtles' behavior in the wild is influenced by handling stress associated with bio-logger attachment and retention. Using animal-borne cameras, this study examined sub-adult and adult green turtles in Australia, and it was observed that turtles exhibited "excessive" swimming right after deployment compared to those recorded after a 24-hour delay. Consequently, whether behavioral changes are observed over shorter periods and if responses are consistent across various life stages is unknown.

Potentially one of the reasons why there is a lack of studies on the impact of bio-logging devices is because studying this phenomenon can present a paradox. If animal behavior is measured using a bio-logger, then it is necessary to consider how to collect the same data on animals without bio-loggers. One way around this issue is to use tools that assess animal behavior remotely and without direct interaction with the target individual. For example, Unoccupied Aerial Vehicles (UAVs) collect visual imagery from an aerial/top-down perspective (Elmeseiry et al., 2021), but in marine habitats, are only suitable for studying large animals in shallow clear waters (Yokota & Matsuda, 2021). UAVs are cost-effective and efficient in evaluating animal behavior, abundance, and distribution (Smith, 2015; Kiszka et al., 2016;

Colefax et al., 2018). Spotting animals via UAVs depends on the UAV's altitude, the size of the species of interest, the resolution of the camera on the UAV, and the magnification of the camera's lens (Bevan et al., 2018). However, it is possible that if a UAV is flown too low, the target animal might sense the UAV's noise and modify their diving behavior. For instance, manatees exhibited strong distress and altered their behavior by fleeing the area, whereas bottlenose dolphins increased reorientation events – defined as changes of group swim direction of 90°or more - when UAVs were flying at 10 meters above them (Ramos et al., 2018; Fettermann et al., 2019). Bevan et al., (2018) concluded that sea turtles seem to not detect UAVs flying at an altitude of 15 m or above. Nevertheless, it is possible that even if the turtles are detecting the UAVs, they are not exhibiting any behavioral response. For instance, Ditmer et al. (2015) observed that black bears did not respond behaviorally by relocating to a different location or increasing their movement rates when UAVs flew in their vicinity (at an average altitude of 21 m), yet black bears exhibited a physiological response by manifesting an increase in heart rate.

One of the simplest bio-logging devices is the time-depth records (TDR), which are typically used to study diving behavior in marine megafauna (Kooyman, 1967; Kooyman et al., 1971; Eckert et al., 1986). When analyzing TDR data, a depth threshold (around 2-5 m) is typically set to define the limit at which a dive is initiated (e.g., Hagihara et al., 2011; Bentley et al., 2021) as most research on air-breathing marine megafauna take into account dives to tens or hundreds of meters. According to Stokes et al. (2023), this method works effectively in deep habitats since the pressure sensor employed has a resolution that enables monitoring a considerably wide range and can record dives down to 1000 m or more. However, in very shallow habitats (< 5m), setting a depth threshold is not feasible since we are not able to accurately determine when the dive initiates or ends due to the small resolution of the pressure sensor. Additionally, it is typically assumed that when the animal is at the surface, it is engaged in breathing. However, this is not necessarily the case, as the animal may not be breathing. In addition, the shape of the dive profiles obtained with TDR data is often interpreted via their shape: U-, V-, and W-shaped dives are typical descriptions (Wilson et al., 1996; Hochscheid et al., 1999). U-shaped dives are typically linked to benthic diving when turtles exhibit resting (Hochscheid, 2014; Stokes et al., 2023). In fact, data from high-resolution bio-loggers show that green turtles, especially at night, do a prolonged series of U-dives in shallow waters, which is thought to be related to resting behavior (Southwood et al., 2003a). These dives have a steep descent, followed by a flat bottom phase, and a steep ascent. V-shaped dives are typically associated with exploration and orientation (Hochscheid et al., 1999; Seminoff et al., 2006), while W-shaped dives are commonly linked to benthic exploration and feeding (Seminoff et al., 2006). However, from just TDR data you cannot directly observe the behavior the animal is engaging in, so they are just suppositions. For instance, depending on the study, these U-shaped dives may be classified as feeding-related behavior instead of resting behavior (Hochscheid et al., 1999).

Therefore, the simplicity of dive profiles obtained by TDRs may have classified some feeding-related behavior as resting behavior. For instance, direct observations by Houghton et al. (2000) revealed that loggerhead turtles, during the same dive, sometimes were feeding on bivalve mollusks and then resting on the seabed. If the study had used a TDR, the resulting profile (U-shaped dive) would have been categorized as resting behavior (Houghton et al., 2000). In fact, it is usual to see green turtles foraging in shallow waters, and they can rest in both shallow and deep waters (Houghton et al., 2003; Southwood et al., 2003a). The same study from Houghton et al. (2000) found a clear contrast when engaging in U-shaped dives, in depth between the foraging and resting sites for juvenile hawksbill turtles. When they had finished their feeding in shallow reef habitats (< 3 m depth), the turtles sometimes would rise to the surface to breathe before descending to a typical depth of 6 to 9 m to rest for up to 30 min. Thus, even if green and hawksbill turtles perform short foraging dives, they often rest on the seabed during the same dive (Houghton et al., 2003; Stokes et al., 2023). In summary, TDR data provide a 2D representation with limited detail that only allows for simplistic interpretations of behaviors (Fedak et al., 2001; Boyd et al., 2004; Halsey et al., 2007). The need to improve the interpretation of diving behavior has led to the diversification of bio-loggers by combining TDRs with integrated sensors, like cameras (Reina et al., 2005; Seminoff et al., 2006) or accelerometers (Wilson et al., 2008; Fossette et al., 2012) that measure additional parameters such as swim speed or path heading (Davis et al., 2003; Sato et al., 2003; Ropert-Coudert & Wilson, 2005; Wilson et al., 2014), which may allow more accurate evaluations of energy management and confirm behaviors assumed by TDRs (Hochscheid, 2014). However, few studies have tried to validate TDR records by synchronizing them with visual observations (Francke et al., 2013).

2. Life-history of green turtles

Green turtles (*Chelonia mydas*) are circumglobally distributed in tropical and temperate habitats (Southwood et al., 2003a; Quiñones et al., 2022). Female turtles will periodically leave the water to nest on sand beaches. After incubating and successfully hatching, hatchlings swim offshore before being entrained in oceanic gyres for several years (Musick & Limpus, 1996; Reich et al., 2007). Turtles will remain in these habitats foraging on invertebrates until juveniles reach approximately 30 to 40 cm carapace length (CL). At this point, they migrate to neritic habitats in tropical and temperate zones (Musick & Limpus, 1996). When reaching maturity, green turtles migrate to reproductive habitats that are typically close to their natal nesting beach (Musick & Limpus, 1996), when most research is conducted (Uribe-Martínez et al., 2021).

3. Foraging ecology of green turtles

Green turtles that come from pelagic to neritic habitats in the Caribbean gradually shift towards an herbivorous diet dominated by seagrasses and/or macroalgae (Esteban et al., 2020). In fact, the primary food source for green turtles in the Caribbean is turtle grass, or *Thalassia testudinum* (Bjorndal, 1996), and they use a cultivation grazing strategy by repeatedly foraging in previously grazed seagrass meadows (Bjorndal, 1996; Constant et al., 2023). Green turtles favor feeding new-growth leaves with lower levels of lignin, which is indigestible and reduces the digestibility of other carbohydrates, and higher levels of nitrogen and protein, making leaves more nutritious for sea turtles (Bjorndal, 1980; Gulick et al., 2021).

Sea turtles influence nutrient cycling and community structure in their foraging habitats (Bjorndal, 1996). As a result, sea turtles play an important role in the functioning of marine ecosystems (Costa, 2007; Constant et al., 2023). For instance, according to Thayer et al. (1982), green turtle grazing reduces the decomposition rates of seagrass leaves because the leaves become smaller and easier for detritivores to consume and enhance the recycling of nitrogen. Moreover, they also translocate nutrients from foraging habitats to nesting beaches (Bjorndal, 2003).

4. Diving physiology and buoyancy control in sea turtles

Sea turtles are among the longest-diving air-breathing vertebrates, being able to dive for over 10 hours in a single dive (Hochscheid, 2014). Sea turtles need to surface to exchange the CO_2 accumulated during the previous dive for O_2 before starting the following dive (Lutcavage & Lutz, 1996; Fahlman et al., 2024). Sea turtles' complex, multichambered lungs enable high tidal volumes and high exploratory flow rates, facilitating the rapid and effective exchange of respiratory gases (Gatz et al., 1987; Lutcavage et al., 1989). These features are beneficial for promoting oxygen uptake to support elevated metabolic rates during prolonged exercise (Southwood, 2013). In fact, cheloniids rely more on their lungs for oxygen storage because they typically only descend to a few tens of meters, compared to other deeper divers who mostly rely on their blood and muscles (Lutcavage & Lutz, 1996; Fahlman et al., 2017; Stokes et al., 2023).

According to Southwood et al. (2003b), the maximum length of a dive is determined by the body's oxygen storage, the proportion of those stores that are used, and the rate at which oxygen is utilized – also known as metabolic rate. However, it has been observed adaptative responses for conversing available oxygen during dives – also referred to as dive response - where sea turtles exhibit peripheral vasoconstriction and severe bradycardia (Berkson, 1966; Thompson & Fedak, 1993; Fahlman et al., 2024). An additional adaptive advantage is the capacity to alter heart rate in response to changing physiological needs (Fahlman et al., 2024). For instance, when sea turtles ascend to the surface to breathe their heart rate increases to facilitate the gas exchange, whereas they exhibit a decrease in heart rate prior to initiating the dive (Fedak & Thompson, 1993; Fahlman et al., 2024). Therefore, sea turtles respond physiologically before initiating a dive, which suggests that they "know" that they are starting a dive.

In addition to using the lungs as an oxygen store, they also help sea turtles adjust their buoyancy (Hochscheid et al., 2003). Since gas compresses with depth due to increasing pressure, sea turtles are able to dive into deeper waters by inspiring a greater volume of air while still achieving neutral or negative buoyancy at the desired depth (Stokes et al., 2023). Therefore, sea turtles can rely on their lung capacity to reach neutral buoyancy at a specific depth (Lutcavage & Lutz, 1996; Hays et al., 2000). This may suggest that sea turtles "know" the desired depth they will reach before starting the following dive. In that case, sea turtles that dive into deeper waters would inspire a greater volume of air, consequently being able to remain submerged for a longer period at a given metabolic rate (Southwood et al., 2003a). This positive correlation between dive duration and depth has been demonstrated in a number of species, such as penguins (Wilson, 2003), dugongs (Churchward, 2001), and sea turtles (Hochscheid et al., 1999). Moreover, the size of the turtle may represent an important factor between both dive duration and depth because bigger sea turtles have a longer oxygen store that would allow them to remain for a longer time and in deeper waters (Lutcavage & Lutz, 1996; Matley et al., 2020).

Diving in shallow waters may theoretically be energetically inefficient for them since to forage at shallow depths the lungs must be filled to a reduced capacity, which leads to individuals to resurface after short intervals (Minamikawa et al., 1997; Houghton et al., 2000; Matley et al., 2020). However, in contrast to this, green and hawksbill turtles dive shallower and shorter dives during the day for feeding, while deeper waters are preferred for nighttime resting (Blumenthal et al., 2009; Hart et al., 2016). This may suggest that in shallow habitats, factors other than buoyancy control may influence diving behavior, such as activity patterns or temperature. However, few studies have been conducted on sea turtles in shallow-water habitats, highlighting the need for further research into the diving behaviors of sea turtles in these environments.

5. Temperature effects on sea turtles' diving behavior and physiology

Temperature has a well-documented effect on green turtle physiology, provoking changes in their diving behavior (Hazel et al., 2009; Iverson et al., 2019; Okuyama et al., 2021). For instance, loggerhead turtles in the North Pacific changed their diving behavior by reducing the depth and duration of their dives when the temperature dropped below 15°C at 20 m, and they stayed most of their time in depths where temperatures were warmer than 15°C (Howell et al., 2010). In another study olive ridley turtles in the tropical Pacific, in response to shifting oceanographic conditions, showed a shift in their depth by staying most of their time above 60 m depth during daytime and at night in order to remain between 22 and 28°C (Swimmer et al., 2006). Seasonal variation in dive behavior has also been observed for juvenile green turtles residing in sub-tropical waters where there are less pronounced temperature differences

(Hochscheid, 2014). For instance, on the east coast of Australia, sea turtles inhabited shallower waters in winter compared to summer (mean summer vs mean winter = 26.2-21.3ºC), doubling their average dive duration (24 min) and tripling their surface intervals (mean 1.8 min) (Southwood et al., 2003a). Whereas in a Florida lagoon, Mendonça (1983) found that juvenile green turtles moved into deeper and cooler waters (lower than 2°C) and exhibited minimal activity (40% less) during the mid-afternoon when summertime temperatures at shallow seagrass feeding meadows exceeded 31ºC. In conclusion, sea turtles consistently seek to remain within the limits of their optimal temperature range, relocating to cooler waters when they perceive the temperature to be excessive and vice versa.

A general trend can be identified indicating a negative correlation between dive duration and temperature (Southwood et al., 2003a; Hatase et al., 2007; Thomson et al., 2012; Matley et al., 2020), although there are differences in the relationships between temperature and dive behavior across species and regions (Hochscheid, 2014). Since sea turtles are ectotherms, this could be because higher temperatures accelerate the oxygen consumption rates due to increased energy demand (Southwood et al., 2006; Hounslow et al., 2022). Moreover, some studies suggest that temperature indirectly impacts diving behavior by influencing associated prey distributions in the water column (Swimmer et al., 2006; Howell et al., 2010). This is because the thermocline is an important factor in the vertical distribution of pelagic prey, which in turn influences the foraging success of marine megafauna species (Hakoyama et al., 1994; Benoit-Bird et al., 2013). For instance, leatherback turtles in the Northwest Atlantic showed shorter and shallower dives in cooler, productive shelf habitats (Dodge et al., 2014) while olive ridleys in the Guiana basin showed an increase in foraging depth with a deeper thermocline and increasing foraging time with lower temperatures (Chambault et al., 2016).

Climate change is significantly raising sea temperature (IPCC, 2007). Given the correlation between temperature and diving behavior, climate change may also influence diving capacity. However, this remains poorly understood (Rodgers et al., 2021). Understanding turtles' diving behavior and its environmental drives is crucial for the identification of key marine areas for conservation strategies (Browning et al., 2017), even with the challenge of predicting behavioral adaptability to environmental variations, especially climate change (Hawkes et al., 2009; Matley et al., 2020). For instance, a 5ºC increase in water temperature has been observed to decrease dive duration by approximately 25% (Matley et al., 2020). Shorter dives could mean a reduction of rest or foraging, and increased time swimming between the seafloor and the surface to breathe, which leads to an energetic increase in the cost of diving (Rodgers et al., 2021). It could even force animals to spend more time near the water's surface, where they are more vulnerable to bycatch since longlines are set between 0 and 100 m (Lewison et al., 2013).

6. Predator risk in sea turtles

Turtles can employ various strategies to elude predators, including rapid swimming or changes in depth and selecting areas with a low frequency of encounters with predators (Heithaus et al., 2008; Hounslow et al., 2020). On the one hand, sea turtles appear more vulnerable to predators during their commute between the surface and the seafloor, where they are most likely to be seen and easily ambushed (Heithaus & Frid, 2003). Thus, during the day, there may be less exposure to visual predators due to the steeper and more active descents and ascents (Lear et al., 2021). Stokes et al. (2023) and Hazel et al., (2009) observed that predators play an important role in influencing habitat selection, with hawksbill and green turtles finding refuge from shark predators in shallow dives. Nonetheless, Hart et al. (2016) found that juvenile green turtles prefer deeper resting places due to energetic benefits that outweigh the expenses of traveling to deep water and increased risk of predation.

7. Aim of the study

The objective of this study is to determine the impact of diverse environmental variables and handling stress on the diving behavior of juvenile green turtles in very shallow waters (< 5 m). This will be achieved by using animal-borne cameras and unmanned aerial vehicles (UAVs).

This study aims to investigate two features: (1) how diving behavior is influenced by bio-logger attachment. Using bio-loggers may influence juvenile green turtles' behavior due to handling stress. Because of the challenge of getting data from sea turtles that have not been handled, we will take "control" data by using UAVs and then compare it with data collected with bio-loggers. By observing how their behavior changes over time after the release and comparing it with our control data, we will be able to determine if handling stress influences their diving behavior. We hypothesize that handling these animals may induce behavioral changes over time until turtles can relax. We expect that, immediately after release, turtles will spend most of their time swimming given the elevated stress levels they will present after the bio-logging attachment. Over time, we expect that swimming time will decrease while resting time will increase.

(2) The factors influencing diving duration in very shallow water habitats. We hypothesize that juvenile green turtles aim to maximize their time spent underwater based on different factors. We expect that larger turtles and deeper dives will increase the dive duration due to their effect on buoyancy; higher temperatures and more active behaviors will decrease the dive duration because of their effect on their oxygen consumption; and larger breath duration will increase the duration of the following dive since turtles will have greater oxygen stores.

8. References

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CHAPTER 2: FACTORS INFLUENCING THE DIVING BEHAVIOR OF JUVENILE GREEN TURTLES IN SHALLOW MANGROVE CREEKS IN THE BAHAMAS

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KEYWORDS

Animal-borne cameras, UAVs, bio-loggers, handling stress, dive duration, sea turtles

Abstract

Animal-borne devices (= bio-loggers) have revolutionized marine megafauna research. Nevertheless, there is limited data on how bio-logger attachment and handling stress affect animals. This study used animal-borne cameras with time-depth recorders to examine short-term diving behavior (< 210 min) and the factors driving dive duration in juvenile green turtles (*Chelonia mydas*) in understudied shallow water habitats (< 5 m depth) in The Bahamas. We compared the behavior of 58 turtles with bio-loggers to 25 non-handled turtles observed by Unoccupied Aerial Vehicles (UAVs), which do not cause panic in turtles. After release, turtles spent 70-80% of their time swimming with a mean dive duration of 45.3 ± 34.3 seconds (SD). Over 90 min, dive duration increased while swimming time decreased until stabilizing. However, the UAV data was similar to turtle behavior immediately after bio-logger deployment, suggesting that bio-loggers and handling stress influence diving behavior for at least 90 min. Afterward, the effect of bio-loggers either: (1) has a small effect and UAVs may produce biased data on "natural" turtle behavior or (2) a longer period of data collection (> 3h) is necessary for turtles to return to non-handled behaviors. This study recorded some of the shortest mean dive durations observed for juvenile green turtles (66.43 ± 75.85 seconds SD). Maximum dive depth, breath duration, and temperature exhibited a statistically significant positive effect on dive duration. Longer breath duration provided more oxygen, allowing longer and deeper dives. Tidal patterns increased temperature when the turtles were already relaxed, which prolonged dive duration despite typically raising metabolic rates. The likelihood of active behavior decreased throughout the dive duration while resting increased, reflecting oxygen use: active behaviors require more oxygen, shortening dives, while resting allows longer dives. In conclusion, juvenile green turtles in shallow waters do not perform long dives, and (2) dive duration is influenced by breath duration and activity patterns.

Introduction

Understanding animal behavior and how animals interact with their environment is one of the key pillars of ecology, which may also contribute to conservation efforts and enhance their welfare (Miller, 1983; Buchanan et al., 2012; Egnor & Branson, 2016). However, marine megafauna such as sea turtles are challenging to track visually as they spend most of their time underwater (Hochscheid, 2014; Hounslow et al., 2022). To address this issue, researchers frequently use animal-borne devices (hereafter referred to as bio-loggers) that generate data on the host animal and its immediate surroundings by recording information about animals' movements, behavioral patterns, physiology, and the environment using devices attached to animals (Rutz & Hays, 2009; Hochscheid, 2014). However, deploying a bio-logging device inherently requires physical interaction with the target animal which may provoke a stress response that could impact their behavior after the release (Flower et al., 2015). Understanding the impacts of bio-logging attachment on animals allows for a better interpretation of the data from bio-logging devices to gain insights into the "natural" behavioral patterns of these animals. However, there is a paucity of studies investigating the potential impacts of this handling stress and bio-logging attachment.

Sea turtles are among the longest-diving air-breathing vertebrates, being able to dive for several hours in a single dive (Hochscheid, 2014). Therefore, studying their diving patterns is a key component in understanding their behavior. The primary oxygen stores for sea turtles are their lungs, but they also play an additional function as buoyancy control as animals that inhale more will be more positively buoyant and vice versa (Lutcavage & Lutz, 1996; Hays et al., 2000). For a diving animal, the most efficient approach to diving may be to reach neutral buoyancy when reaching the depth at which this animal will spend most of the dive. However, when an animal descends below the surface, the buoyancy reduces due to increasing hydrostatic pressure (Hays et al., 2004; Hochscheid et al., 1999). Thus, the deeper the dive, the greater the volume of oxygen required by the turtle, which consequently requires an extended period on the surface to breathe. This suggests that for an animal to reach neutral buoyancy, it must "know" which depth it will descend to on its next dive and inhale an appropriate amount of air. Moreover, given that the turtle will have a greater volume of oxygen, the duration of the dive will also increase. In fact, there seems to be a correlation between the number of breaths and submergence time on the proceeding dive (Lutcavage & Lutz, 1991; West et al., 1992; Fahlman et al., 2024). As such, diving in shallow waters may theoretically be energetically inefficient for them since the lungs must be filled to a reduced capacity, which leads to individuals to resurface after short intervals (Minamikawa et al., 1997; Houghton et al., 2000; Matley et al., 2020). However, sea turtles are frequently observed in shallow waters (e.g., Hays et al., 2002; Houghton et al., 2003; Hart & Fujisaki, 2010), which suggests that additional factors than buoyancy may influence their diving behavior in shallow habitats, such as temperature or activity patterns. Despite this, little is known about the diving behavior of juvenile green turtles in very shallow-water habitats.

Temperature has a well-documented effect on green turtles, with a general trend identified indicating a negative correlation between dive duration and temperature (Southwood et al., 2003; Hatase et al., 2007; Thomson et al., 2012; Matley et al., 2020). For instance, Matley et al. (2020) observed that a 5°C increase in water temperature decreased dive duration by approximately 25%, while Rodgers et al. (2021) found a decrease of approximately 11% in dive duration for every 1°C increase in temperature. Since sea turtles are ectotherms, this is change in dive duration probably because higher temperatures accelerate the consumption of oxygen reserves due to increased energy demand (Southwood et al., 2006; Hounslow et al., 2022). These reductions in dive duration could provoke changes in diving behavior such as a reduction of rest, social interactions, or foraging (Rodgers et al., 2021).

To study sea turtle behavior, several different techniques have been used (Hart et al., 2016). The use of bio-loggers has revolutionized the field of behavioral ecology by enhancing our understanding of the physiology, behavior, and ecology of certain marine megafauna (Kooyman, 2004; Ropert-Coudert et al., 2009). Time-depth recorders (TDR) are arguably some of the simplest bio-loggers used for marine research and were developed to measure the depth and duration of an animal's dives (Hart et al., 2016). However, TDRs do not provide detailed information on the type of activity undertaken while submerged – a dive profile alone may not reveal whether the turtle is swimming, resting, or feeding while at the seabed (Houghton et al., 2000). Moreover, when analyzing TDR data, a depth threshold is typically set to define the limit at which a dive is initiated (e.g., Hagihara et al., 2011; Bentley et al., 2021). This method is not feasible in very shallow habitats (< 5 m) since it is not possible to accurately determine when the dive initiates or ends due to the resolution of the pressure sensor. To address this issue, TDRs can be combined with other sensors that provide more information about the diving profiles, such as cameras (Reina et al., 2005; Seminoff et al., 2006) or accelerometers (Wilson et al., 2008; Fossette et al., 2012). Yet, there is still a paucity of studies using bio-loggers on diving behavior in very shallow waters.

Deploying bio-logging devices inherently requires some form of interaction with the animal, which can provoke a stress response. In fact, some studies suggest that sea turtles presented higher levels of corticosterone a few hours after being captured (Gregory et al., 1996), which is a common indicator of stress in wild animals (Baker et al., 2013). In turn, this has implications for both animal welfare and the representation of their behavior collected by the bio-logger (McMahon et al., 2012; Flower et al., 2015). In addition to handling stress, a turtle's behavior may be influenced by the physical attachment of the bio-logging device due to increased drag, which can affect their swimming efficiency (Jones et al., 2011). Therefore, it is crucial to determine the extent of the impact of handling stress and bio-logging attachment on the diving behavior of the target organism, as this will facilitate the interpretation of the data obtained and provide insight into the “natural” behavioral patterns of sea turtles. Consequently, a growing number of studies are calling for more empirical research on this matter (Wilson et al., 2018; Williams et al., 2020). However, to date, only one study by Thomson & Heithaus (2014) directly assessed how the behavior of turtles in the wild is influenced by handling stress associated with bio-logger attachment. Specifically, this study deployed animal-borne cameras on sub-adult and adult green turtles in Australia, and it was observed that turtles exhibited “excessive” swimming immediately after deployment compared to those recorded after a 24-hour delay.

Designing experiments to assess how handling stress and bio-logger attachment affect an animal’s behavior can be challenging since we must collect “baseline” behavioral data from individuals who have not been handled and do not have bio-loggers. One way to circumvent this issue is to use methods that allow for remote recording of animal behavior such as Unoccupied Aerial Vehicles (UAVs), which can collect visual imagery from an aerial/top-down perspective (Elmeseiry et al., 2021). UAVs are a cost-effective tool in wildlife conservation, management, and research that are mainly used to monitor organisms that are challenging to observe directly (Ivošević et al., 2015). When flying above wild animals, the distance between the UAV and the animal can be particularly important. Too far away may be difficult to perceive the animal or its behavior. Too close the animal may respond behaviorally or physiologically to the presence of the UAV. Bevan et al. (2018) suggested that sea turtles do not detect UAVs flown at altitudes over 15 m. However, Ditmer et al. (2015) observed in black bears that even in the absence of a panic response when UAVs flew at an average altitude of 21 m, target organisms exhibited a physiological response by increasing their heart rate.

Here, we used a combination of animal-borne cameras, TDRs, and UAVs to (1) characterize the dive behavior of juvenile green turtles in very shallow habitats (< 5 m), (2) to determine the influence of environmental variables on dive duration, and (3) to determine how turtle's behavior may be impacted by bio-logger deployment and retention using data from UAVs to quantify when turtles returned to "normal" behavior patterns.

Materials and methods

Study site. This study was conducted from September 2018 to March 2020 on the southern part of the island of Eleuthera, in The Bahamas. Here, animal-borne cameras were deployed on juvenile green turtles caught in five localities: Starved Creek, Deep Creek, Rollins Creek, Half Sound, and Savannah Sound (Fig. 2.1.). These habitats had a maximum depth of around 5 m and were mostly muddy, algal, seagrass (mainly *Thalassia testudinum*), rocky, and mangrove environments. While Starved Creek faces the Great Bahamas Bank – an expansive carbonate platform with an average depth of 10 m (Buchan, 2000) – Half Sound and Savannah Sound are facing the Atlantic Ocean. Facing the Exuma Sound, Deep Creek, and Rollins Creek are located between the Atlantic Ocean and the Great Bahamas Bank (Buchan, 2000).

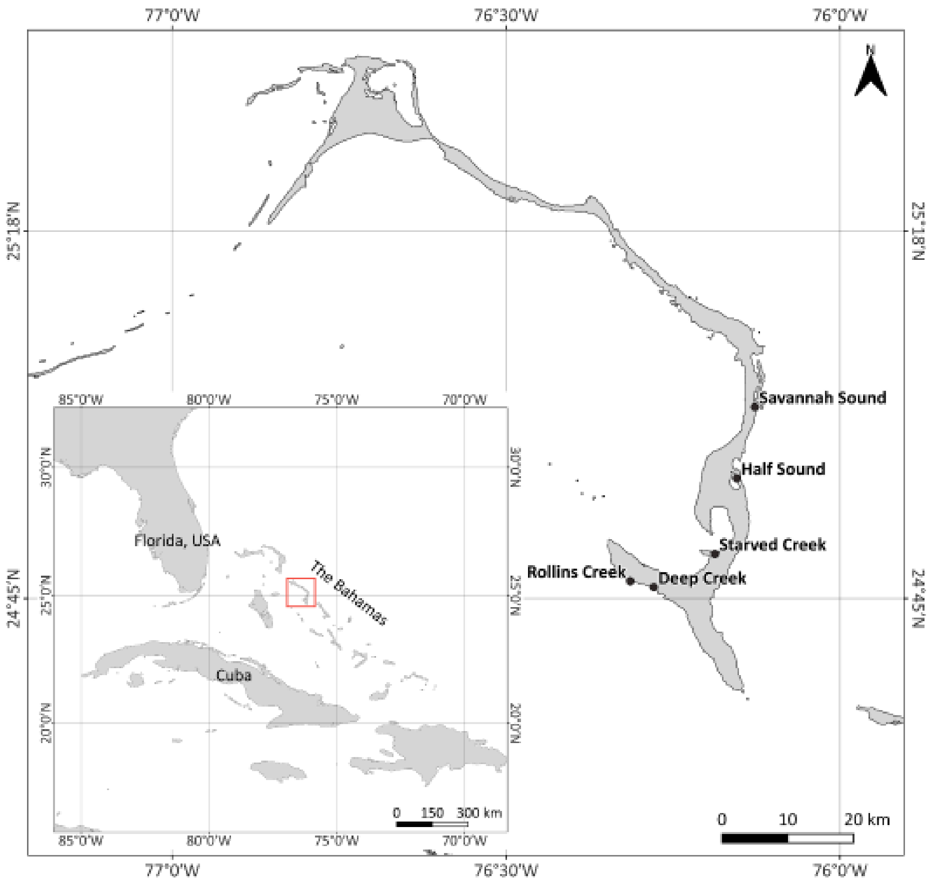

Fig. 2.1. Map indicating the study sites in Eleuthera. The red square indicates the location of the island in The Bahamas. Coastline based on data provided by the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) (https://www.ngdc.noaa.gov/mgg/shorelines/).

TurtleCam Deployment. Juvenile green turtles were captured following the procedures described by Ehrhart & Ogren (1999). For hand-capture, individuals were spotted and subsequently approached by boat until they were within a few meters of research team. Snorkelers then entered the water and attempted to grasp the turtles at the base of their front flippers before being brought onboard the boat. When seine netting, a seine net was placed across chokepoints in the creek system while a group of people (> 10) would start splashing and walk towards the net to direct turtles into the net. Eventually, the seine net would be closed in a circle and then turtles could be hand-captured. Turtles were examined for external injuries, abnormalities, and identification tags. When tags were absent, uniquely numbered metal Inconel tags were deployed to their front flippers. Photos were also taken for photo-identification (Mills et al., 2023). The measurements of Straight Carapace Length and Width (SCL and SCW) were obtained using calipers, while measurements of Curved Carapace Length and Width (CCL and CCW) were obtained using flexible tape.

Turtles larger than 30 cm in SCL, with no visible injuries or abnormalities, were selected for deployment of animal-borne cameras (Fig. 2.2.) - hereafter referred to as TurtleCams. TurtleCams were made by attaching a VHF radio transmitter (MOD-050-2, Lotek, USA) to a dive camera (DiveCamera+, Paralenz, Denmark) and then adding enough rigid foam to ensure the unit was positively buoyant. The TurtleCams had a buoyancy of less than 100 g. The dive camera measured temperature and depth per second with an accuracy of + 0.1°C and + 0.1 m. To attach the TurtleCam, a 5-minute epoxy (KwikWeld, USA) was used to affix three 4 × 4 cm pieces of plastic mesh to the turtle's carapace. Two pieces were placed at the front of the carapace, while the third piece was placed along the midline but towards the back of the carapace. Galvanic timed-releases (AA2, International Fishing Limited, New Zealand) were attached to each piece of plastic mesh with zip ties and then to the TurtleCam with a second zip tie. The process of attaching a TurtleCam took between 15 and 30 minThe galvanic timed-releases corrode when exposed to seawater after a predetermined duration (typically within 3-4 h), allowing the TurtleCam to be released from the turtle and float to the surface. Finally, a unidirectional antenna and a VHF radio receiver could be used to triangulate the location of and recover the TurtleCam.

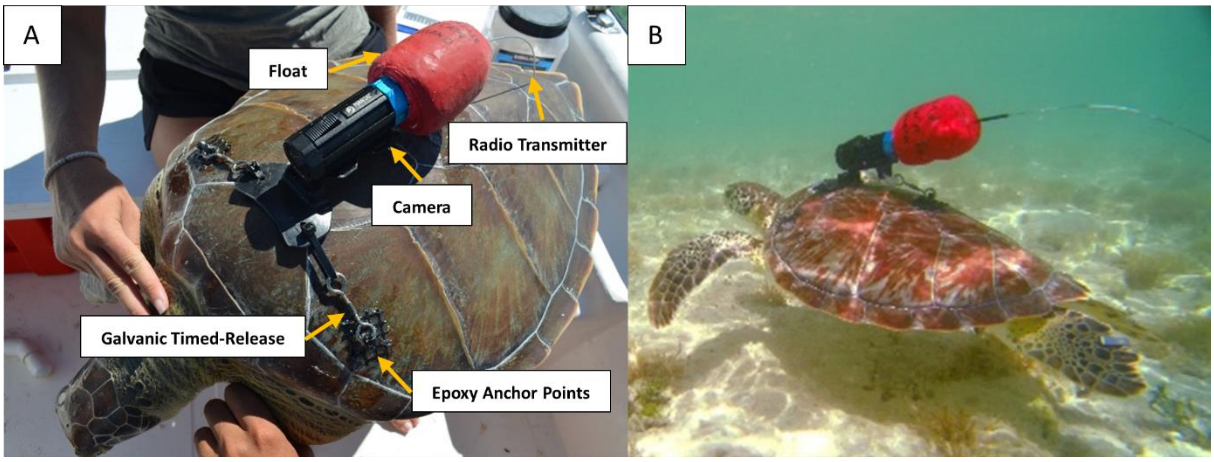

Fig. 2.2. (A) Image of the TurtleCam and the attachment mechanism to a sea turtle's carapace. (B) A free-swimming green turtle with a TurtleCam attached.

Turtles were released within 100 m of their capture location. To prevent any behavioral responses induced by the presence of the boat prior to TurtleCam detachment, the boat was maintained 1 km from the turtle's release location until it was identified that the device was popped-off the turtle. All turtle captures were conducted between 10:00 and 14:00 to minimize the effect of diel patterns on their behavior (Hounslow et al., 2022). After recovering the TurtleCam, the recorded footage was downloaded.

UAV Methodology. Surveys using a DJI Mavic 2 Pro Unoccupied Aerial Vehicle (UAV) were carried out opportunistically at the same creeks in which TurtleCams were deployed. At the beginning of each survey, a 50 cm ruler was placed at ground level and filmed via the UAV at an altitude of 15 m. The length of this ruler (in terms of pixels) was then used as a reference to determine the SCL of any turtle sighted on the survey.

The UAV was flown at 30 m altitude until a turtle was spotted, at which point the camera was set perpendicular to the water's surface. The research team then began recording and aimed to keep the turtle in the center of the frame for a minimum of 10 min or until the battery life was depleted. This process was repeated up to three times per day per creek. Consecutive surveys in the same creek were conducted in separate areas to avoid potentially recording the same turtle multiple times. Furthermore, surveys were conducted on different days from TurtleCams to ensure that the turtles recorded were not handled by us in the previous 24 h. UAV surveys were carried out between 10:00 and 17:00 to match with TurtleCams, as the latest deployment was at 14:00 with a possible recording of up to 3 h.

Video Analysis. I analyzed the diving behavior of juvenile green turtles using footage obtained from the TurtleCam and UAVs, annotating only the diving behavior if over 2h or 10 min of footage was available per turtle, respectively. The following behaviors were categorized: swimming, surfacing, resting, feeding, socializing, and others (Table 2.1.). A single observer analyzed the video to ensure consistency in the categorization of behaviors and minimize subjective interpretations, a single observer analyzed the videos. Furthermore, a single 10-min segment of each TurtleCam footage was randomly selected to annotate its behavior a second time. This was done to compare the labeling second by second and to identify any inconsistencies greater than 5%. If such inconsistencies were found, the entire video was analyzed again.

Table 2.1. Ethogram describing the different behavioral categories for the TurtleCam footage.

Behavior	Description of Behavior
Swimming	The turtle propels itself through the water using its flippers. The front flippers move simultaneously or independently without touching the floor. This includes the time between breaths if the turtle keeps moving.
Surfacing	It begins when the turtle raises its head above the water's surface. It will end when the turtle's nostrils submerge again and, importantly, it begins to actively swim away from the surface. As such, it could include several individual breaths if the animal remained at the surface between breaths.
Resting	The turtle is not actively swimming or crawling (i.e., lack of movement from the front flippers). This included when turtles were resting on the sea floor or under substrate. It does not include resting at the surface between breaths (as this would be considered surfacing).
Feeding	The turtle's feeding behavior can be observed through its head movements, such as biting, chewing, and/or swallowing food. The turtle could also be seen lowering its head and grasping seagrass within the beak.
Socializing	Whenever two or more turtles interacted by approaching, following, circling, or biting.
Others	Any behavior not listed above. Typically, this was either digging or crawling.
No visual	When the camera is covered or the flippers and neck are not correctly observed, avoiding a correct behavior identification.

Turtles were classified as small and large based on a 50 cm SCL threshold that was chosen as a mid-point between the minimum (SCL: 32.6 cm) and maximum size (SCL: 63.7 cm) size of the captured turtles. For UAV turtles, a margin of error of 5 cm accepted (Piacenza et al., 2022) since, at that time, more accurate methodologies were not yet available.

Following the behavior analysis, I did a diving analysis by categorizing when the turtles were either in apnea or breathing into different diving and breathing events, respectively. Diving events were defined as apnea behavior between breaths, whereas breathing events were identified by the rise of the turtle's head above the water surface. It was considered as a single breathing event when the turtle stayed at the surface, either swimming or resting between breaths, until the beginning of a new diving event identified when the turtle actively swam away from the surface. Every breath the turtles took during a breathing event was counted. The TurtleCam footage for each diving event was analyzed to record the maximum dive depth, number of breaths before and after each dive, the behavior conducted per second, and the time after the liberation of the turtle. The duration and the mean temperature of each diving and breathing event were also calculated.

Statistical Analyses. Prior to conducting the statistical analyses, the depth data were calibrated to adjust for sensor variation. To ensure an offset correction across the entire depth profile for each TurtleCam, the turtles' diving profiles were recalibrated by cross-referencing the TDR data with the animal-borne camera footage. The water surface was determined as the zero-reference point, which was identified by the turtle's head rising above the water surface in the videos. The initial "burst" swimming – identified as the first diving event after turtle release - was only considered for the behavioral frequency analysis; it was not included in the rest of the statistical analyses.

The TurtleCam data has been used to visually represent the dive duration in relation to the maximum dive depth, mean temperature of each dive, the breath duration preceding each dive, and the behaviors conducted during each diving event. Additionally, the effect of these variables (along with body size and time since the release) on the dive duration was determined using different Generalized Linear Mixed Models (GLMMs). All statistical analyses were conducted using R software (*version 4.4.2*).

Taking into account the possible effects of body size, a multi-level model (hereafter referred to as the handling stress model) was employed to examine the effects of the handling stress on the dive duration over time up to a maximum of 210 min after TurtleCam deployment. Rather than using raw times of each dive, I decided to pool the dives of each turtle during each post-release 30-min segment and use the center point of the segment as the input value for time (e.g., 15-min for the 0-30 min period). By narrowing the variability, the stability of the model increases but the sample size decreases to one data point per turtle in each 30-min segment. This way, I avoided a) an irregular shape of the curve; and b) an increased weight placed on the first observations immediately after the release, when the turtles performed multiple short dives in short sequence.

A second multi-level model (hereafter referred to as the dive variation model) was employed to investigate the effects of the mean temperature, the maximum dive depth, and the breath duration on the dive duration. Finally, a third multi-level model (hereafter referred to as the dive behavior model) was employed to evaluate the effects of the dive duration on the behavior conducted during the dives. Behaviors described in Table 2.1. were grouped into feeding, resting, and active; being the last one a combination of swimming, socializing, and others. In both the dive variation and the dive behavior models, the potential impact of each individual turtle was considered.

To estimate the full distribution of the model's parameters and quantify support for and against the null hypothesis (Kruschke, 2021), a Bayesian approach was used. The simulations of the models were performed using a Markov Chain Monte Carlo approach (MCMC). For the first model, based on the assumption that dive duration would eventually reach a plateau, a logarithmic model (Eq. 1.) was used with an uncorrelated random intercept varying slopes between turtle size classes (i.e., small and large).

Eq. 1 $$Dive\ duration = \beta_0 + \beta_1 \cdot \ln(Time) + b \cdot \ln\,(Time \parallel Size)$$

where β_0 corresponds to the model's intercept, β_1 to the effect of time, and b to the interactions between the intercept and time with size (as random effect).

For the dive variation model (Eq. 2.), I used gamma regression to constrain the possible predictive outcomes to non-negative ranges, as the response variable is strictly non-negative and correlated random intercepts and slopes between different TurtleCams.

$$\textbf{Eq. 2} \quad Dive\ duration = \beta_0 + \beta_1 \cdot Temperature + \beta_2 \cdot \ln(Depth) + \beta_3 \cdot \ln(Time) + \beta_4 \cdot \ln(Breath\ duration) + b \cdot TurlteCam$$

where β_0 corresponds to the model's intercept, β_1 to the effect of mean temperature, β_2 to the effect of the maximum dive depth, β_3 to the effect of time, β_4 to the effect of the breath duration before a diving event, and b to the random effect of the different TurtleCams.

Finally, the dive behavior model (Eq. 3.) was a Dirichlet regression between the different turtle behaviors expressed as proportions and dive duration.

$$\textbf{Eq. 3} \quad Behavior = \beta_0 + \beta_1 \cdot Dive\ duration + b \cdot TurlteCam$$

where β_0 corresponds to the model's intercept, β_1 to the effect of dive duration, and b to the effect of the different TurtleCams.

After an initial analysis, I determined weakly informative priors for the intercept ($\beta_0 \sim N(-30, 20)$) and time ($\beta_1 \sim N(20, 10)$) for the handling stress model, as the default ones ($\beta_1 \sim N(0, 2.5)$) did not provide enough computational stability fot he model to converge I ran a total of 4 MCMCs of 3000 iterations each (ie., 1000 warm-up and 2000 sampling) in the R package "rstanarm" (Goodrich et al., 2020). For the dive variation model, I used the default priors for both intercept and the other coefficients, and I ran 4 MCMCs of 12000 iterations (i.e., 10000 warm-up and 2000 sampling) each in "rstanarm". Finally, for the dive behavior model, which was run in the R package "brms" (Bürkner, 2017), I used the priors described in the Supplementary Table S1 and ran 4 MCMCs of 12000 iterations (i.e., 10000 warm-up and 2000 sampling. The difference in the length of the MCMCs between the handling stress model and the other two models were due to the availability of computational resources at the time, and I stopped at 3000 as the chains converged at a satisfactory degree. On the other hand, the complexity of dive variation and dive behavior models (many predictors and many responses, respectively) meant that only 3000 iterations would not yield reliable results. Density plots were used to visually represent the full posterior distributions of the models' coefficients, and 89% Credible Intervals (CI) were estimated for each coefficient instead of the more traditional

95% intervals, as they offer more computational stability and better handling of Type-S error (Gelman & Carlin, 2014; Kruschke, 2014).

The models were examined for the presence of outliers by using the Leave-One-Out Information Criterion (LOOIC). This estimate compares the posterior distribution after iteratively leaving one point out from the full one (with all data points included) and is based on the model's Expected Log Predicted Density (ELPD) and the Pareto-Smoothed Importance Sampling (PSIS) method (Vehtari et al., 2017; 2021). Sensitivity tests were performed to determine the effect of the selected priors on the model's outcome (i.e., refitting with antagonistic priors and comparing). Moreover, the percentage of credible model solutions that were practically equivalent to the null hypotheses was measured by using the equivalence test of the overlap between the Region of Practical Equivalence (ROPE) and the 89% High-Density Interval (HDI, in this case identical to the CIs) (Kruschke, 2018). Finally, Bayes Factors (Savage-Dickey density ratio; (Wagenmakers et al., 2010) were calculated for each coefficient to quantify the evidence against or in support of the alternative hypothesis H_1 against a complementary alternative hypothesis H_{-1} (i.e., the positive effect of each predictor on the outcome vs. the negative effect, instead of a null hypothesis H_0 of no effect at all). The R packages "loo" (Vehtari et al., 2017) and "bayestestR" (Makowski et al., 2019) were used to calculate the Bayes Factors and perform diagnostics.

Results

58 TurtleCams were successfully deployed and recovered. These included 31 from Starved Creek, 15 from Rollins Creek, 8 from Deep Creek, 3 from Half Sound, and 1 from Savannah Sound. Out of the 58 turtles, 29 were below 50 cm SCL and 29 were above 50 cm SCL (range: 32.6 cm to 63.7 cm; mean: 49.7 ± 6.9 cm SD). This resulted in 10,438 min (174.9 h) of TurtleCam footage (range: 122 to 202.5 min; mean 180 ± 17 min SD) where sea turtles exhibited very short dives duration (range: 4 to 881 seconds; mean: 66.43 ± 75.85 seconds SD).

During the same period, 25 turtles were filmed using UAVs: 4 in Starved Creek, 6 in Rollins Creek, 6 in Deep Creek, and 9 in Half Sound. This resulted in 379 min (6.3h) of footage (range: 10 to 20 min; mean: 15 ± 2.93 min SD) where sea turtles exhibited very short dives duration (range: 6 to 338 seconds; mean 72.92 ± 59.57 seconds SD). Of these 25 turtles, we estimated that 16 were under 50 cm SCL and 9 were over 50 cm SCL. Hereafter, turtles ≤ 50 cm SCL will be referred to as "small" and those > 50 cm SCL will be referred to as "large".

Handling stress. Immediately after release, all turtles with TurtleCam showed an abrupt "burst" swimming response that was characterized by rapid flipper beats. This response typically only lasted for a few seconds (range: 6 to 110 seconds; mean: 47.46 ± 29.1 seconds SD). Both small and large turtles spent 84% of their time swimming for the first 30 min after being released (Fig. 2.3.). For small and large turtles, surfacing represented 8% and 7% of the next common behavior during this period, respectively. All other behaviors represented less than 5%. The only behaviors that differed small from large turtles by more than 1% were feeding (small: <1%; large: 2%) and resting (small: 5%; large: 3%).

Between 30 and 60 min, the amount of time that small and large turtles spent swimming decreased to 61% and 59%, respectively. For both small and large turtles, the time spent feeding and resting increased over three-fold. Small turtles spent 20% of their time resting and 1 % feeding, while large turtles spent 22 and 8 % of their time resting and feeding, respectively. By 60 to 90 min, swimming time decreased (small: 52%; large: 44%) while resting time increased (small: 29%; large: 37%).

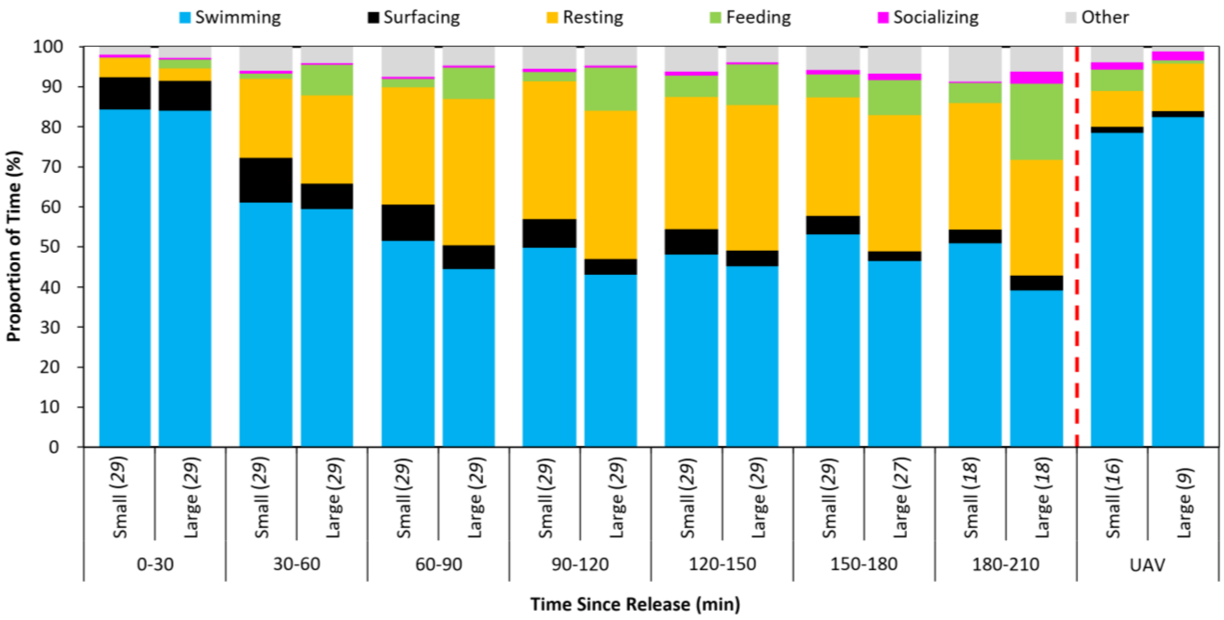

Fig. 2.3. Percentage of time spent by juvenile green turtles of different size classes (small: ≤ 50 cm SCL; large: > 50 cm SCL) conducting different behaviors (see legend above graph) after the deployment of an animal-borne camera. The final pair of columns represent comparable data collected on individuals without bio-logging devices via Unoccupied Aerial Vehicles. Numbers in parentheses correspond to the respective sample size *n*.

After 90-120 min and until 180-210 min, the amount of time spent swimming, resting, and feeding remained relatively constant. Specifically, swimming time spent for small turtles was 48-53%, and for large turtles was 39-48%; resting time for small turtles was 29-34% and for large turtles was 29-37%; feeding time was 2-6% and 9-19% for small and large turtles, respectively. Only two behaviors – surfacing and socializing – showed a noticeable change after 90 min. For both small and large turtles, the surfacing showed a continual decrease until it reached a minimum of 3.4 and 3.7% for small and large turtles, respectively. In contrast, socializing time remained < 1% in small turtles but increased up to 3% in large turtles.

Overall, for both small and large turtles, the proportion of time spent conducting each behavior was similar. The main difference was that, after 120-150 min, the feeding time of small turtles appeared to plateau at 10%, whereas large turtles consistently increased over time. Additionally, typically large turtles spent more time swimming while small turtles spent slightly more time surfacing and swimming.

The identified behavior from turtles recorded by UAV showed similarities between small and large turtles, with high levels of swimming (78 and 82% for small and large turtles, respectively). Although this was roughly similar to the time spent swimming between 0-30 min after the deployment of a TurtleCam, turtles recorded by UAV spent less time surfacing (2%

for both small and large turtles), and spent more time feeding (5 and 2% for small and large turtles, respectively) and socializing (1 and 2% for small and large turtles, respectively).

Starting with the first model diagnostics, all Pareto's K values were below the 0.7 threshold, indicating the absence of any outliers that could affect the outcome (all k values were < 0.5 and classified as "good"). In terms of sensitivity to the priors, the percentage of deviation for the Maximum A Posteriori probability estimate (MAP) was 1.24% when fitting with antagonistic priors, thus indicating robustness.

Regarding the assessment of the model's outcome (Table 2.2.), the Bayes Factor (BF) of the coefficients for the intercept (β_0) and time (β_1) were within the ranges that indicate "strong" evidence (BF > 10), and the remaining coefficients – those that represent the effect of turtle size on the intercept and time – were negligible. Based on the high overlap between the 89% HDI and the ROPE, the equivalence test confirmed that there was no significant size effect on the dive duration over time. There was a small percentage of overlap for β_0 and β_1 probably because the % HDI in ROPE's metric is highly conservative as it interprets any overlap between the credible values of a coefficient and the Region of Practical Equivalence (i.e., values that may be equivalent to zero) as potentially nullifying significance (Kruschke, 2018). In addition, it is highly sensitive to differences in scales or units between the predictors and the response. In this case, I can safely assume that this is a matter of the difference in time scales between the predictor (time) and the outcome (dive duration) variables (i.e., minutes and seconds, respectively). I assumed that the units used were coherent with the nature of the studied phenomenon. However, the difference in scale may affect what is considered a "negligible change", which is essential in defining the ROPE. This is why, even given the minimal percentages of overlap that give confidence in the outcome of the model, it was decided to put the dive variation model on the same scale. Finally, 150 min after release, the curves and intervals predicted by the handling stress model appear to be higher than the measured dive durations for both turtle sizes. This could be explained by the reduced sample size of these last 30 min segments (i.e., data for fewer turtles for 150-180 min and 180-210 min), which may have placed more weight on earlier times.

Table 2.2. Coefficients of the logarithmic model, with SE, 89% Credible Intervals (CI), Bayes Factors (BF), and the percentage of the HDI in the Range of Practical Equivalence (%HDI in ROPE). Note that CI and HDI values are identical, but the original terminology is maintained. BF values between 3.2-10 constitute "Substantial" evidence in favor of the alternative hypothesis H_1 (i.e., positive effect) while values > 10 indicate "Strong" evidence (Kass & Raftery, 1995). The respective ranges in favor of the complementary alternative hypothesis H_{-1} (i.e., negative effect) are 0.3-0.1 and < 0.1. BF values ranging from 0.3 to 3.2 are considered trivial against the null hypothesis H_0 (i.e., no effect). % HDI in ROPE other than 0 indicates "non-decisive" evidence (Kruschke, 2018).

Model Parameter	Estimate	SE	5.5% CI	94.5% CI	BF	% HDI in ROPE
β_0 - Intercept	-62.17	39.52	-146.17	17.42	**0.09**	5
β_1 – ln(time)	42.32	12.80	2.94	82.03	**21.13**	2
β_2 – Intercept:Size "S"	-2.30	23.69	-91.68	63.95	0.77	43
β_3 – ln(time):Size "S"	3.20	24.01	-59.13	97.20	1.46	42
β_4 – Intercept:Size "L"	0.77	9.56	-37.81	42.44	1.30	68
β_5 – ln(time):Size "L"	-0.91	9.37	-43.70	35.34	0.73	67

The measured dive duration of the two size classes (i.e., "small" and "large") are shown in Fig. 2.4. at each 30-min segment after release. Overlayed predictions for continuous time are also shown, based on the means of 1000 posterior draws of the model, and finally, UAV measurements. The two most noticeable features are: 1) the overlap of the posterior intervals for both turtle sizes, which is consistent with the trivial effect of turtle size on the model's outcome based on the equivalence test values and Bayes Factors; and 2) the measured and estimated dive duration based on TurtleCams when approaching the plateau phase (i.e., "normal behavior") are notably higher (double) than the respective UAV values used as "control". The estimates of the model coefficients are represented in the lower panel (Fig. 2.4.) (see also Table 2.2.), where β_0 and β_1 ± SE do not cross the 0 line.

The full posterior distributions for each model coefficient as well as a diagnostic figure of the 4 MCM chains are provided as Supplementary materials.

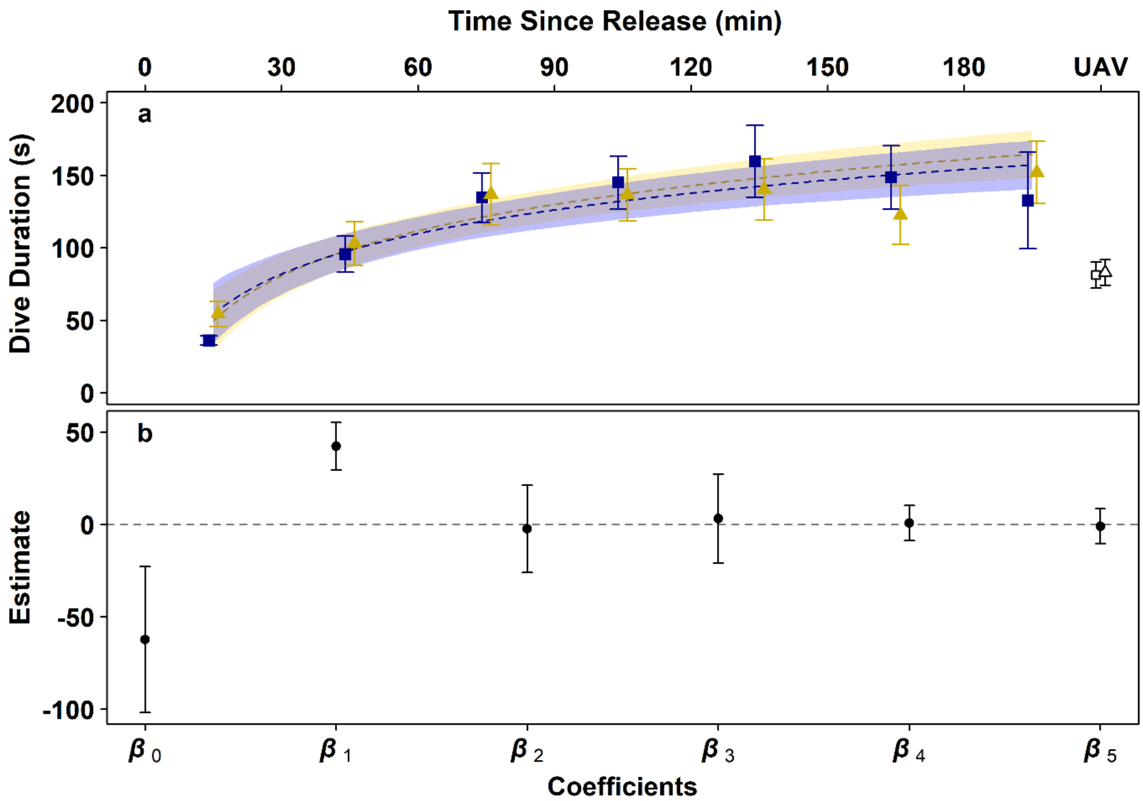

Fig. 2.4. Dive duration of juvenile green turtles of different size classes after the attachment of an animal-borne camera or determined via Unoccupied Aerial Vehicles. Upper panel (a): measured mean dive duration ± SE for small (yellow triangles) and large (blue squares) turtles during each 30-min post-release segment. Hollow symbols at the right side of the panel correspond to the respective measurements with the UAV and do not follow the timeline. Dashed curves indicate the predicted dive durations for continuous time based on the model. Shaded bands represent the 89% posterior intervals. Lower panel (b): logarithmic model coefficient estimates ± SE (see also Table 2.2.). The dashed line marks 0 (i.e., no effect).

Effect of habitat parameters and previous breathing patterns on dive duration. All of Pareto's K values for the dive variation model were found to be below 0.5, which is indicative of a "good" fit (i.e., compared to the 0.7 threshold). This suggests the absence of outliers that could affect the model's outcome. Regarding the sensitivity to the priors, the percentage of deviation for the MAP when fitting with antagonistic priors was 0.58% for the mean temperature, 0.17% for the depth, 0.18% for the time since the release, and 0.09% for the breath duration, confirming the robustness of the model to the choice of priors. In assessing the model's outcome, the Bayes Factors (BF) of the coefficients for mean temperature (β_1), maximum dive depth (β_2), time since the release (β_3), and previous breath duration (β_4) were found to fall within the range's indicative of "strong" evidence (BF > 10) in favor of the alternative hypothesis H_1 (i.e., positive effect on the dive duration). The model's intercept (β_0) was also significant (although negative). The coefficients for the different 58 TurtleCam IDs can be found in Supplementary Table S2, where the model showed variability in dive duration between some individuals. The equivalence test confirmed that all variables significantly affected the dive duration since the 89% HDI and the ROPE did not overlap. A summary of the model metrics is presented in Table 2.3.

Table 2.3. Coefficients of the logarithmic model, with SE, 89% Credible Intervals (CI), Bayes Factors (BF), and the percentage of the HDI in the Range of Practical Equivalence (%HDI in ROPE). Note that CI and HDI values are identical, but the original terminology is maintained. BF values between 3.2-10 constitute "Substantial" evidence in favor of the alternative hypothesis H_1 (i.e., positive effect) while values > 10 indicate "Strong" evidence (Kass & Raftery, 1995). The respective ranges in favor of the complementary alternative hypothesis H_{-1} (i.e., negative effect) are 0.3-0.1 and < 0.1. BF values ranging from 0.3 to 3.2 are considered trivial against the null hypothesis H_0 (i.e., no effect). % HDI in ROPE other than 0 indicates "non-decisive" evidence (Kruschke, 2018).

Model Parameter	Estimate	SE	5.5% CI	94.5% CI	BF	%HDI in ROPE
β_0 - Intercept	-3.36	0.33	-3.89	-2.84	**$1.94 \cdot 10^{-12}$**	0
β_1 – Mean Temperature	0.19	0.01	0.17	0.21	**$8.76 \cdot 10^{25}$**	0
β_2 – ln(Depth)	0.66	0.01	0.64	0.69	**$3.84 \cdot 10^{64}$**	0
β_3 – ln(Time Release)	0.24	0.004	0.23	0.25	**$1.14 \cdot 10^{84}$**	0
β_4 – ln(Breath Duration)	0.17	0.007	0.16	0.18	**$3.99 \cdot 10^{33}$**	0

Fig. 2.5. illustrates the predicted effect on the dive duration of different variables - (a) maximum dive depth; (b) mean temperature; and (c) breath duration. The figure shows the effect of these variables at each 10-minute segment after release, in the form of separate curves for the 5th (lower curves), 50th – mean (middle curves), and 95th (upper curves) percentile of the variable in question. It also shows the overlayed predictions for the continuous time, based on the means of 1000 posterior draws of the model for a new random (i.e., simulated) turtle individual. It can be observed that there is a positive effect of the maximum dive depth, the mean temperature, and the previous breath duration on the dive duration. This is in accordance with the strong effect of all the variables on the model's outcome, as determined by Bayes Factors and the equivalence test. Furthermore, the greatest variance between the 95% and 5% percentiles is observed for the maximum dive depth variable, followed by the mean temperature and breath duration with CI overlapping most of the time (except the 5% CI for the depth). Finally, as with the handling stress model, the dive duration presents a logarithmic curve that reaches a plateau that remains relatively stable over time. The lower panel (d) of Fig. 2.5. graphically represents the estimates of the model

coefficients (see also Table 2.3.), with all the coefficients ± SE not crossing the 0 line (indicating significance).

The full posterior distributions for all model coefficients, along with a diagnostic figure of the 4 MCMC chains, are provided as Supplementary materials.

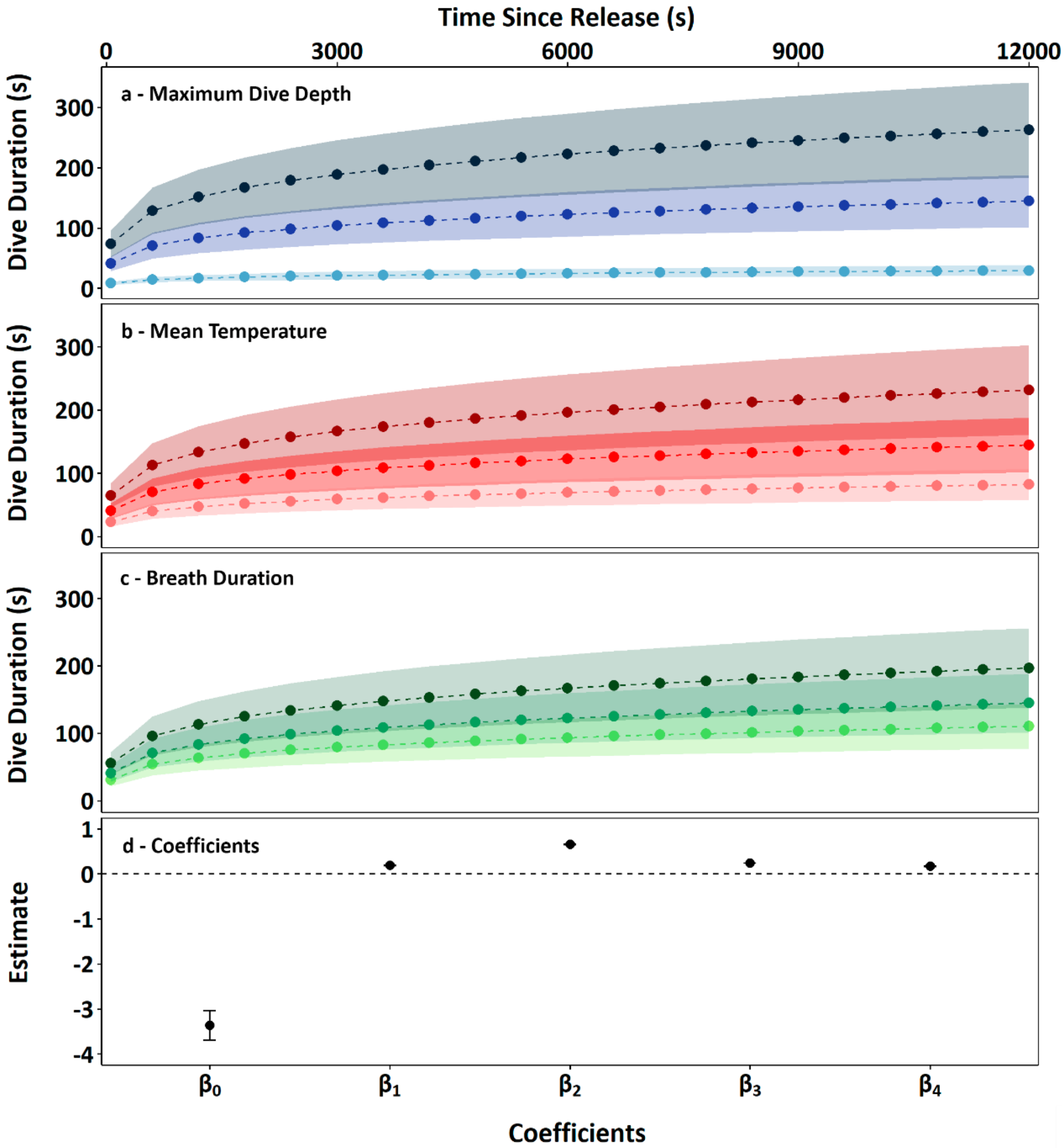

Fig. 2.5. Predicted effect on the dive duration of different variables after attaching an animal-borne camera. (a): measured dive duration of the 95% (darker, upper circles), mean (medium circles), and 5% (lighter, lower circles) of our maximum dive depth data during each 10' post-release segment. Dashed curves indicate the predicted dive durations for continuous the based on the model and are accompanied by 89% posterior intervals (shaded bands). (b): measured dive duration of the 95% (darker, upper circles), mean (medium circles), and 5% (lighter, lower circles) of our mean temperature data during each 10' post-release segment. Dashed curves indicate the predicted dive durations for continuous the based on the model and are accompanied by 89% posterior intervals (shaded bands). (c): measured dive duration of the 95% (darker, upper circles), mean (medium circles), and 5% (lighter, lower circles) of our breath duration data during each 10' post-release segment. Dashed curves indicate the predicted dive durations for continuous the based on the model and are accompanied by 89% posterior intervals (shaded bands). (d): logarithmic model coefficient estimates ± SE (see also Table 2.3.). The dashed line marks 0 (i.e., no effect).

Maximum dive depth. Dive duration remained relatively constant for dives between 0 and 1.5 m depth, with a mean duration of less than 100 seconds and minimal variability (Fig. 2.6.). At greater depths, the mean dive duration increased gradually, accompanied by an increase in variability. After 4.3 m, there were single diving events at 4.4 m, 4.7 m, and 6.1 m, which show a similar tendency of increasing dive duration throughout the different depths. Overall, there was a positive correlation between dive duration and depth.

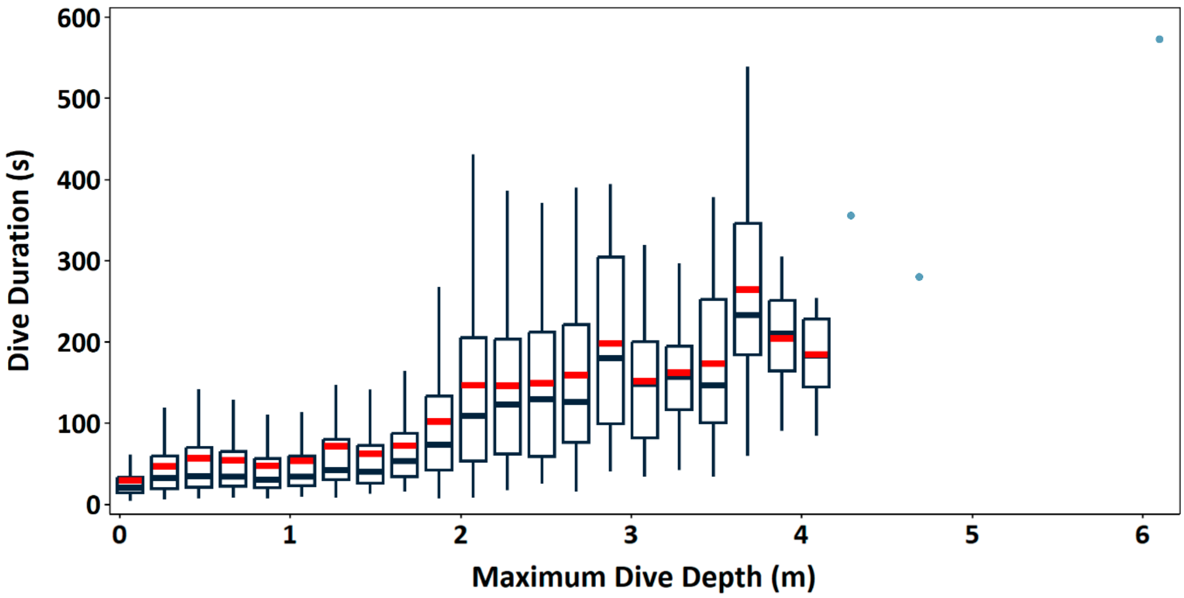

Fig. 2.6. Dive duration of different diving events at different maximum dive depths from juvenile green turtles with animal-borne cameras. Each boxplot is grouping the depth into 0.2 m bins, from 0.1 m to 4.3 m. Dark blue lines and red horizontal represent the median and the mean of each boxplot, respectively. Light blue points are datapoints (single diving events at those depths). The relationship is shown descriptively without statistical analysis.

Mean temperature. Dive duration at temperatures between 21 and 22°C was notably prolonged compared with the dive duration exhibited over 24°C, with a mean dive duration between 300 and 500 seconds (Fig. 2.7.). However, the dataset is relativity limited in that range, which may contribute to the observed variability. At temperatures above 22ºC, the mean dive duration decreased to below 150 seconds. This remained relatively constant between 24 and 34°C and presented considerably less variability. Above 34°C, there was not enough data (one diving event per degree °C) to calculate the mean dive duration; however, these diving events remained relatively constant to the means observed between 24 and 34 °C, with diving events lasting below 150 seconds. Overall, data suggest a negative correlation between dive duration and sea temperature (contrary to the outcome of the model, see the Discussion section below for further details).

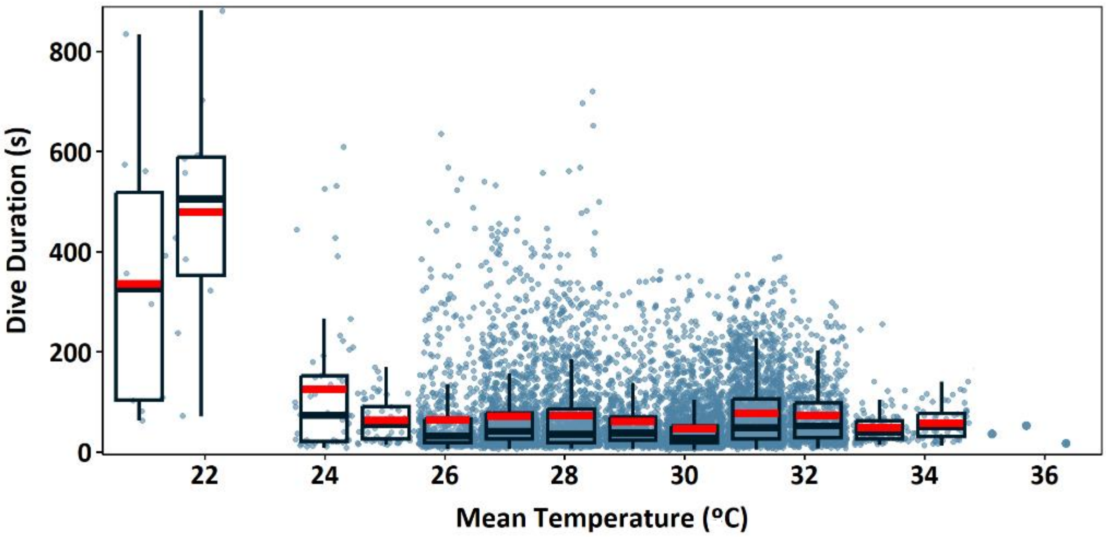

Fig. 2.7. Dive duration of different diving events at different temperatures from juvenile green turtles with animal-borne cameras. Each boxplot is grouping the temperature into 1°C bins, from 21°C to 34°C. Dark blue and red horizontal lines represent the median and the mean of each boxplot, respectively. Light blue points are the datapoints (single diving events at those temperatures). The relationship is shown descriptively without statistical analysis.

Breath duration. Fig. 2.8. illustrates the relationship between dive duration and the time spent breathing immediately prior to a dive. A logarithmic relationship is observed between both variables, with an initial increase in dive duration at short breath durations until reaching a plateau of approximately 200 seconds of dive duration at 40 seconds of breath duration. Additionally, the variability of the data appears to gradually increase with the breath duration. Above 120 seconds of breath duration, there was not enough data (one diving event per 10 seconds of breath duration) to calculate the mean dive duration.

Effect of dive duration on different behaviors during the dive. As with the previous models, all of Pareto's *K* values of the dive behavior model were below 0.5, indicating a "good" fit, with no apparent outliers. It was no possible to assess the model's sensitivity to priors, as for some coefficients flat priors were used instead of a distribution (i.e., all number in (-∞, ∞) are a priori equally probable). This practically means that there are by default no antagonistic values to compare to. In terms of the outcome, feeding behavior was used as the benchmark against which the other two behaviors (i.e., active and resting) were assessed. This selection is a technical

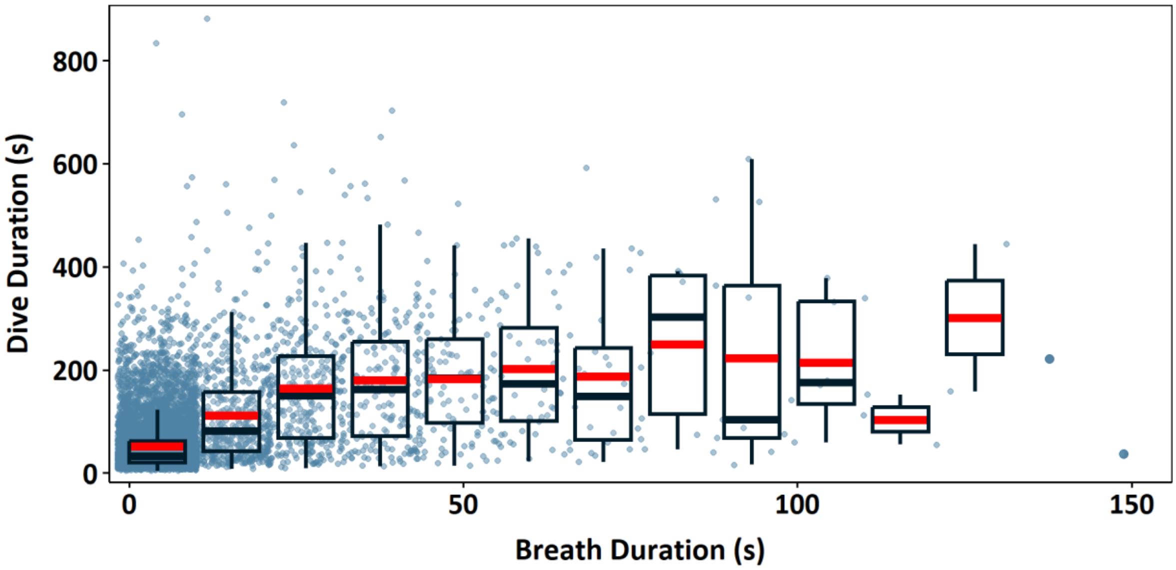

Fig. 2.8. Effect on the dive duration of the breath duration of the previous diving event from juvenile green turtles with animal-borne cameras. Each boxplot is grouping the breath duration in bins of 10 seconds, from 1 to 150. Dark blue and red horizontal lines represent the median and the mean of each boxplot, respectively. Light blue points are the datapoints (single diving events). The relationship is shown descriptively without statistical analysis.

detail of modeling categorical variables, and which category is selected does not actually affect the outcome of the model in terms of relationships, only the sign and value of the calculated coefficients. The Bayes Factors (BF) of the coefficients for the intercept comparing active with feeding behavior (β_0) and the comparison between resting and feeding behavior (β_3) were found to fall within the range indicative of "strong" evidence (BF > 10) in favor of the alternative hypothesis H_1 (i.e., positive effect on the probability). In contrast, the BF for the intercept comparing resting and feeding behavior (β_1) and the comparison between active and feeding behavior (β_2), fell within the ranges in favor of the complementary alternative hypothesis H_{-1} (i.e., BF < 0.1; negative effect on the dive duration). The coefficients for the different 58 TurtleCam IDs can be found in the Supplementary Table S3. The equivalence test confirmed that only the β_0 and β_1 significantly affected on the probability of presenting a different behavior from feeding since the 89% HDI and the ROPE did not overlap, while β_2 and β_3 presented a 100% overlap. This is probably due to the same factors given for the handling stress model, which are also applicable to this model. Moreover, the dive behavior model relies on a comparison of the various behaviors exhibited, with one behavior (in this case, feeding behavior) selected as the reference point for comparison. The discrepancy in units (seconds vs. probability) may be influencing the outcome of the ROPE in an analogous way to that observed in the handling stress model. Furthermore, the shape of the active behavior curve, despite being represented on a different scale, is notably similar to the feeding behavior curve shape. This probably contributes to the estimation of 0 for active behavior as observed in Table 2.4. In contrast, the resting behavior curve exhibits an inverse shape to the feeding behavior curve, with a positive proportion of 0.01 (see Table 2.4.) between the two.

Table 2.4. Coefficients of the Dirichlet model, with SE, 89% Credible Intervals (CI), Bayes Factors (BF), and the percentage of the HDI in the Range of Practical Equivalence (%HDI in ROPE). Note that CI and HDI values are identical, but the original terminology is maintained. BF values between 3.2-10 constitute "Substantial" evidence in favor of the alternative hypothesis H_1 (i.e., positive effect) while values > 10 indicate "Strong" evidence (Kass & Raftery, 1995). The respective ranges in favor of the complementary alternative hypothesis H_{-1} (i.e., negative effect) are 0.3-0.1 and < 0.1. BF values ranging from 0.3 to 3.2 are considered trivial against the null hypothesis H_0 (i.e., no effect). % HDI in ROPE other than 0 indicates "non-decisive" evidence (Kruschke, 2018).

Model Parameter	Estimate	SE	5.5% CI	94.5% CI	BF	%HDI in ROPE
β_0 – Intercept:Active	3	0.03	2.95	3.05	**$5.69 \cdot 10^{179}$**	0
β_1 – Intercept:Resting	-0.27	0.04	-0.35	-0.19	**$1.13 \cdot 10^{-7}$**	0
β_2 – Active	0	0	0	0	$5.56 \cdot 10^{-7}$	100
β_3 – Resting	0.01	0	0.01	0.01	$4.86 \cdot 10^{7}$	100

Fig. 2.9. illustrates the predicted probability of presenting different behaviors (feeding, active, and resting) depending on the dive duration. The upper panel (a) shows the overlayed predictions for the continuous dive duration, based on the means of 1000 posterior draws of the model. It can be observed that as the dive duration increases, the probability of presenting a resting behavior also increases, while the active behavior decreases at the same time. In contrast, the feeding remains relatively constant throughout the dive duration. The lower panel (b) graphically represents the estimates of the model coefficients (see also Table 2.4), with only the coefficient β_0 not crossing the 0 line. The Discussion section "Methodological remarks" will go into further detail about the fact that these observations do not match the coefficients.

The full posterior distributions for each model coefficient as well as a diagnostic figure of the 4 MCM chains are provided as Supplementary materials.

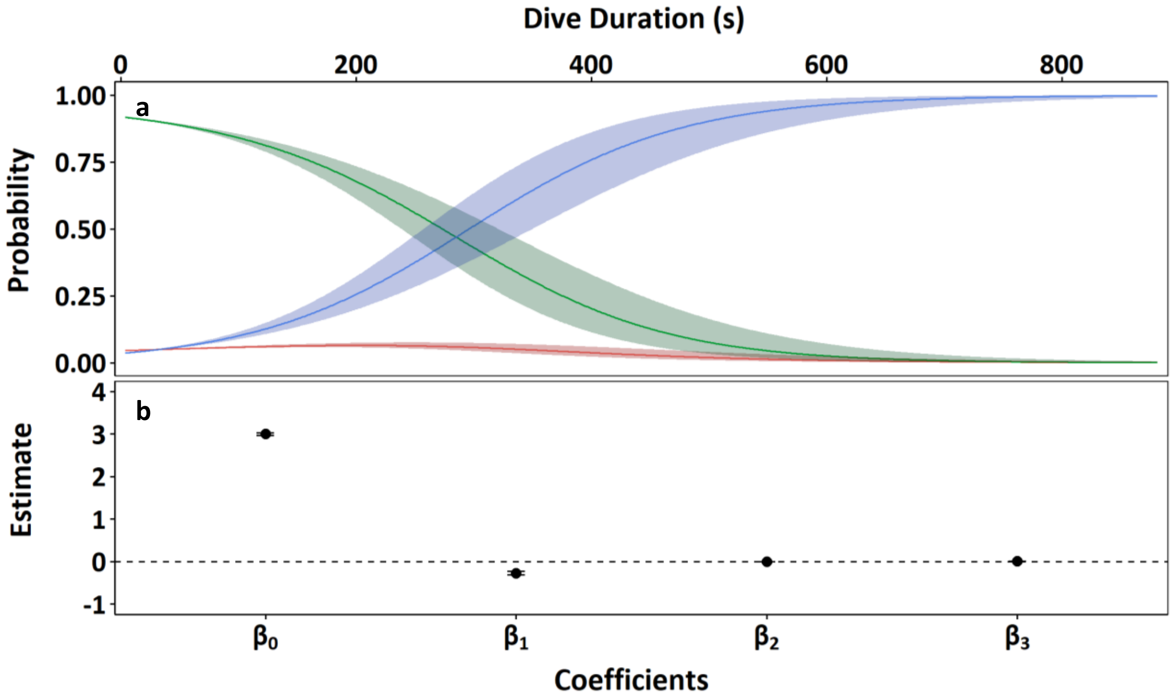

Fig. 2.9. Predicted probability of turtles to display different behaviors throughout the dive duration. **(a):** Curves indicate the predicted probabilities of feeding (red), active (green) and resting (blue) behaviors for continuous dive duration and are accompanied by 89% posterior intervals (shaded bands). **(d):** Dirichlet model coefficient estimates ± SE (see also Table 2.4.). The dashed line marks 0 (i.e., no effect).

Discussion

Handling stress. In this study, I assessed the effects of bio-logger attachment and handling stress on the short-term behavior of juvenile green turtles using UAVs and animal-borne cameras. While the most conspicuous stress response that I observed was undoubtedly the abrupt "burst" swimming response exhibited by turtles for the first seconds after release, it should be noted that the amount of time turtles spent swimming was notably higher in the first 30 min post-release and did not appear to reach a plateau until 90 min had passed. This suggests that studies that consider "burst" swimming responses as indicators of a disturbance response in sea turtles may overlook less apparent indicators of stress, such as elevated swimming frequency, particularly in the context of handling stress but also in the presence of snorkelers (e.g., Griffin et al., 2017; Siegfried et al., 2023) or UAVs (e.g., Bevan et al., 2018). Considering that every turtle was released within 100 m of their encounter location, this elevated swimming is unlikely to reflect a homing response. Rather, it is most likely a prolonged "flight" response meant to evade the perceived threat location.

After 90-120 min post-deployment, the proportion of time that turtles spent swimming reached a plateau between 40 and 50%. At this point, the mean dive duration and resting behavior also reached a plateau between 30 and 40%. This was also observed in the handling stress model, where dive duration increased initially over time until reaching a plateau at approximately 60 min, suggesting that turtles have returned to "normal" behavior patterns that are no longer influenced by handling stress. Particularly, feeding times are similar to larger green turtles in Australia when recorded using animal-borne cameras with a 24 h delayed start function (Thomson & Heithaus, 2014). Moreover, if I combine my data on swimming with other active behaviors including feeding, socializing, and surfacing, then turtles in my study spent around 70% of their time being active after the plateau at 90 min post-release. Similar results were obtained using tri-axial accelerometers that collected data for 2 to 5 days for juvenile green turtles in Florida, showing 73% of their time being active (Hart et al., 2016).

One of the goals was to represent the behavior of unhandled turtles without bio-loggers attached by using the UAV data as a "control". It was therefore assumed that any patterns of behavior or mean diving rates observed in the TurtleCam data over time would gradually approach the values acquired in the UAV surveys. Instead, the UAV surveys showed that the turtles were swimming for more than 80% of the time, and their mean dive duration was similar to the first 30 min after an animal's release after the attachment of a TurtleCam. Additionally, the UAV survey data do not appear to fall within the projected ranges of the corresponding curves as derived in Fig. 2.4. One hypothesis to explain this pattern would be that juvenile green turtles require an extended rest period than my sampling window (i.e., > 210 min) because of the stress involved in handling and deploying bio-logging devices. Sometime after this point, the turtles may then start to increase their activity rates again to exhibit behavioral patterns similar to those observed during UAV surveys. This, however, may be improbable given that previous studies on green turtles using animal-born cameras with delayed start functions (Thomson & Heithaus, 2014) or tri-axial accelerometers (Hart et al., 2016) over several days collected data showing similar activity patterns that were observed after 90-120 min post-deployment.

A second hypothesis that could account for the high levels of swimming observed in the UAV footage is that there may be a bias in the random UAV surveys used to find turtles toward turtles that are actively swimming. Moving animals are typically easier to identify than stationary ones (Duffy et al., 2018), and the TurtleCams also showed that turtles often rest under overhanging structures they would be obscured from the UAV's perspective.

A third hypothesis is that the nearby presence of a UAV may cause juvenile green turtles to increase their swimming activity even if does not cause a "burst" swimming response. In fact, noise levels from low-flying UAVs can be perceived by marine organisms when close to the surface (Christiansen et al., 2016) and there is some, albeit inconclusive, evidence that suggests sea turtles actively avoid low-frequency sounds such as airguns (DeRuiter & Larbi Doukara, 2012) and boat engines (Tyson et al., 2017). Although I think the second hypothesis is most probable, the first and third hypotheses also deserve consideration and further study. It should be noted that the second and third hypotheses are not mutually exclusive.

It should be mentioned that most turtles were observed shifting back and forth while resting under the substrate because of the wave activity at the study site. I think that the prevailing current flow caused these passive movements, and I was unable to identify any clear evidence of turtles actively trying to "scratch" the bio-logger from the carapace. As a result, I am not able to demonstrate that turtles can detect the presence of the bio-logger. I believe that handling stress, rather than any stress related to the device's replacement, is primarily responsible for the behavior changes that have been observed post-bio-logger deployment.

Differences in body size. There were no statistically significant differences observed between the mean dive duration of large and small turtles recorded using both TurtleCam and UAVs. Furthermore, both small and large turtles exhibited similar trends in behavioral patterns over time, suggesting that body size does not affect the response to and recovery from handling stress in juvenile turtles within the SCL range sampled here (range: 32.6 cm to 63.7 cm; mean: 49.7 ± 6.9 cm SD). Nevertheless, smaller turtles always spent more time swimming and surfacing and less time resting and feeding relative to their larger counterparts. It could be possible that large turtles are able to remain for longer periods resting and feeding due to their larger oxygen stores. However, this would also result in a statistical difference in dive duration between the two size classes, which was not observed. It could be also plausible that the longer periods of swimming observed in small turtles are partly influenced by the higher potential for predation risk. However, very shallow waters lead to the exclusion of large sharks, as evidenced by the few potential predations observed in any of the surveyed areas and no large sharks were spotted in the TurtleCam footage.

Dive duration. The dive variation model in Fig. 2.5. used a Bayesian mixed model to quantify the effect of mean temperature, maximum dive depth, time since the release, and breath duration on juvenile green turtles' post-release diving behavior. All four variables were found to have a positive effect on dive duration. The time since release (i.e., handling stress) exhibited the highest BF, followed by the maximum dive depth, the breath duration, and the mean temperature (see Table 2.3.). The influence of the time since release on the dive duration can be observed in the resulting curves, which exhibited a comparable shape to what was observed in the handling stress model (i.e., a logarithmic curve), with an initial pronounced increase in dive duration until they reached approximately 3000 seconds (equivalent to 60 min), at which point the increase became more moderate.

The positive effect of maximum dive depth and the breath duration on the dive duration is also observed in Fig. 2.6. and, to a lesser extent, in Fig. 2.8., respectively. It is possible that the dive duration could have increased with depth and breath duration due to their buoyancy regulation through the lungs. Since gas compresses with depth, by diving into deeper waters with a greater inspired lung volume, sea turtles can still achieve neutral buoyancy at the desired depth (Southwood et al., 2003; Stokes et al., 2023). This may suggest that sea turtles "know" the desired depth they will reach before starting the following dive. In that case, sea turtles that dive into deeper waters would inspire a greater volume of air, consequently being able to remain submerged for a longer period (Southwood et al., 2003). In fact, there appears to be a correlation between the number of breaths taken and the duration of submergence on the proceeding dive (Lutcavage & Lutz, 1991; West et al., 1992; Fahlman et al., 2024). Therefore, if the turtle is aware that the subsequent dive will occur at a greater depth, it may prolong the breathing duration to enhance lung oxygen storage. This phenomenon has been observed in other studies, where a significant correlation was found between the maximum dive duration and the maximum dive depth (Hart et al., 2016). Additionally, this has also been observed in other species, including penguins (Sato et al., 2002) and sea lions (McDonald & Ponganis, 2012). This correlation is also influenced by the fact that it takes longer to reach deeper depths. However, in my study, as it placed very shallow habitats, the impact of reaching depth is negligible. This could also explain the fact that my results showed some of the shortest dive durations ever observed in shallow habitats compared to other studies (e.g., Houghton et al., 2000; Thomson et al., 2012; Chambault et al., 2016), with a mean dive duration of 66.43 ± 75.85 seconds SD.

In sea turtles, dive duration and temperature of water typically have a negative correlation. This is because higher temperatures accelerate the oxygen consumption rates due to increased metabolism (i.e., increased energy demand), which results in the turtle being unable to remain underwater for longer periods (Southwood et al., 2006; Hounslow et al., 2022). This phenomenon is also observed in Fig. 2.7., which shows a decrease in dive duration from 300-500 seconds to less than 150 seconds as temperature increases. However, the mean temperature in the dive variation model showed a positive correlation, indicating that an increase in mean temperature resulted in an increase in dive duration. One potential explanation for this discrepancy is that the limited data available between 21 and 22ºC (Fig. 2.7.) may introduced a bias, leading to an artificially trend where dive duration decreases with increasing temperature. However, Southwood et al. (2003) have demonstrated a decrease in dive duration when turtles were exposed to elevated temperatures, ranging from 21 to 26°C. Similarly, Matley et al. (2020) observed comparable results with an increase in temperature from 26 to 30°C. A second hypothesis is related to the tidal patterns observed at the study site. Given that TurtleCams were always released between 10:00 and 14:00 in mangrove creeks, the tide fall was experienced by the turtles after approximately one hour from the release. During the tide fall, the warm waters from the mangroves flow to the ocean, resulting in an increase in temperature for sea turtles. At this point, turtles have already had 1 hour to relax since the handling, and their dive duration begins to increase, despite the rising temperature. Fig. S7 in the Supplementary Materials illustrates the temperature increase over time for each TurtleCam, and in most cases, this occurs one hour after the release.

Dive behavior. Regarding the dive behavior model, a Bayesian mixed model was used to quantify the effect of the dive duration on juvenile green turtles' post-release diving behavior (expressed as the probability of presenting either of three observed behaviors). Although there are certain limitations to my approach (which were discussed in the previous section), as with most in situ studies involving real specimens, I am confident in the validity of my results.

Fig. 2.9. illustrates that the probability of exhibiting active behaviors declines over the dive duration, the probability of resting increases, and the probability of feeding remains relatively constant. One hypothesis to explain the observed decrease in the probability of being active could be that the increased oxygen consumption is associated with the turtle's active state (Southwood et al., 2003), which in this study encompasses a range of activities including swimming, socializing, and others. This elevated oxygen consumption may subsequently reduce the probability of undertaking long dives with an active behavior. This may also apply to the higher probability of presenting a resting behavior in longer dives. Since the turtle is not active, its oxygen consumption is reduced, allowing it to remain submerged for longer. Similarly, Houghton et al. (2000) observed that resting dives lasted longer than active or foraging dives.

A second hypothesis, not exclusive from the first one, is that sea turtles may be aware that their subsequent dive will involve a period of rest, prompting them to breathe more deeply to prolong their submergence. This is related to the observation that the breath duration before a dive increases with the duration of the dive, a phenomenon that has been discussed in this study and other studies, such as Fahlman et al. (2024). Additionally, in case turtles are breathing more before a resting dive, it may result in a deeper dive due to the greater volume of air in their lungs since they will need to descend deeper to reach neutral buoyancy. This has also been observed in other studies such as that conducted by Houghton et al. (2000), which found that resting dives were significantly deeper than active and foraging dives. With regard to the feeding behavior probability that remained relatively constant in the model, it is plausible that turtles are not eating as they could due to the stress experienced from the deployment of the TurtleCams. However, it is also possible that, given the prolonged digestive process of seagrass (Bjorndal, 1980), turtles only feed a limited amount at a time and then rest while digesting.

Conclusions

My results suggest that within 90 to 120 min post-release, the behavioral effects of handling stress and bio-logger attachment on juvenile green turtles are significantly reduced. While I hypothesize that this is unlikely to have any discernible impact on long-term survival rates, it would be prudent for further research to examine how the elevated swimming response and initial absence in feeding behavior influence the daily energetic budgets of turtles. Furthermore, the elevated activity patterns I observed in the UAV patterns highlight some uncertainty in my results. Specifically, they highlight the need for more research using animal-borne cameras that can film for longer than my 210 min maximum, as well as studies investigating the capacity of low-flying UAVs to enact subtle changes in the behavior of sea turtles. I can see benefits, for both scientists and wild animals, in creating new methods to assess and reduce potential stressors when working with wild animals.

This study observed dive durations that were notably shorter than those reported in other studies, which was likely due to the shallow nature of the study site. Furthermore, my results indicated a positive effect of the maximum dive depth, and the breath duration on the dive duration of juvenile green turtles, suggesting that they “plan” dives by adjusting their breathing based on the expected depth of the following dive. In contrast to the typical negative correlation between temperature and dive duration, I found a positive effect between these two variables. This discrepancy was likely due to the influence of the tidal fall during the first hour. It could be interesting to investigate how different variables affect dive duration after the initial 3000 seconds. This would allow us to avoid the tidal effect but also to avoid the handling stress that occurs during that time.

Finally, my results indicated that the probability of being active decreases with dive duration while resting behavior becomes more likely. This could be associated with oxygen consumption, but it could also be plausible that turtles may "plan" a rest dive and breathe more deeply, enabling longer dives. It could be interesting to examine whether resting dives also involve deeper dives, given that larger breaths could result in deeper dives due to the effect of the buoyancy.

Acknowledgments

A huge thanks is extended to countless researchers, interns, and students at the Cape Eleuthera Island School for their essential help with fieldwork. The TurtleCam project was funded by the Cape Eleuthera Institute, Western Connecticut State University (WCSU), and WCSU's Finding Our Way project. This latter project was supported by the National Oceanic and Atmospheric Administration's National Marine Fisheries Service and Office of Education through its New England B-WET Program to TP (NA16NMF0080003). NJR was funded by the Spanish government (AEI) through the Ramon y Cajal postdoctoral program (#RYC2021-034381-I). DC was funded by a Juan de la Cierva Formación Postdoctoral Fellowship (Ref: FJC2021-047734-I, a MCIN/AEI/10.13039/501100011033, and a European Union NextGenerationEU/PRTR funds). JMRG was funded by the Juan de la Cierva postdoctoral program (Ref: JDC2022-050085-I).

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Supplementary materials

Priors – Dive behavior model. For the dive behavior model, I used the priors described in Table S1.

Table S1. Table of the priors used in the behavior model. If a grouping factor (in this case, the TurtleCam ID) has several group-level effects, then Lkj (1) priors are used to estimate the correlation matrices between those effects. Student-t priors are used to provide at least some regularization to increase convergence and sampling efficiency while they are only weakly informative to influence as few results as possible. Here, student-t priors have 3 degrees of freedom and a scale parameter that depends on the SD of the response, which is 2.5. The Gamma prior is set because the *dirichlet* family needs additional parameters to be estimated, and "Gamma (0.01, 0.01)" is prior by default. There are different parameter classes: (1) "b" refers to the population-level effects and does not affect the intercept, (2) "cor" is used to set the same prior on every correlation matrix, and (3) "sd" refers to the SD of varying coefficients. Finally, "dpar" refers to the distributional parameter, in this case, the active or resting behavior (Bürkner, 2017).

Prior	Class	Coefficient	Group	dpar
Lkj (1)	cor			
Lkj (1)	cor		TurtleCam ID	
Normal (0,1)	b	Dive Duration		Active
Normal (0,1)	b	Dive Duration		Resting
Gamma (0.01, 0.01)	phi			
Student-t (3,0,2.5)	SD	Dive Duration	TurtleCam ID	Active
Student-t (3,0,2.5)	SD	Dive Duration	TurtleCam ID	Resting
Student-t (3,0,2.5)	SD	Intercept	TurtleCam ID	Active
Student-t (3,0,2.5)	SD	Intercept	TurtleCam ID	Resting

Bayesian model coefficients – TurtleCam IDs. The coefficients for the different 58 TurtleCam IDs from the dive variation model are presented in Table S2.

Table S2. Coefficients of the random effects from the logarithmic model, with standard error (SE), 89% Credible Intervals (CI), Bayes Factors (BF), and the percentage of the HDI in the Range of Practical Equivalence (%HDI in ROPE). Note that CI and HDI values are identical, but the original terminology is maintained. BF values between 3.2-10 constitute "Substantial" evidence in favor of the alternative hypothesis H_1 (i.e., positive effect) while values > 10 indicate "Strong" evidence (Kass & Raftery, 1995). The respective ranges in favor of the complementary alternative hypothesis H_{-1} (i.e., negative effect) are 0.3-0.1 and < 0.1. BF values ranging from 0.3 to 3.2 are considered trivial against the null hypothesis H_0 (i.e., no effect). % HDI in ROPE other than 0 indicates "non-decisive" evidence (Kruschke, 2018).

Model Parameter	Estimate	SE	5.5% CI	94.5% CI	BF	%HDI in ROPE
β_5 – TurtleCam 2	-0.17	0.1	-0.33	-0.1	0.045	20
β_6 – TurtleCam 3	-0.29	0.1	-0.45	-0.14	**0.001**	0
β_7 – TurtleCam 5	0.16	0.1	0.01	0.32	20.58	22

Continued

β_8 – TurtleCam 6	0.47	0.1	0.31	0.62	**$8.80 \cdot 10^{4}$**	0
β_9 – TurtleCam 7	0.5	0.1	0.34	0.65	**$2.95 \cdot 10^{5}$**	0
β_{10} – TurtleCam 8	0.32	0.1	0.15	0.48	**956.69**	0
β_{11} – TurtleCam 9	-0.09	0.09	-0.24	0.07	0.227	56
β_{12} – TurtleCam 10	0.75	0.1	0.59	0.9	**$3.47 \cdot 10^{8}$**	0
β_{13} – TurtleCam 11	-0.98	0.09	-1.13	-0.84	**$3.64 \cdot 10^{-15}$**	0
β_{14} – TurtleCam 12	0.02	0.1	-0.15	0.18	1.27	74
β_{15} – TurtleCam 13	-0.25	0.11	-0.43	-0.07	0.014	4
β_{16} – TurtleCam 14	0.47	0.11	0.29	0.64	**$2.06 \cdot 10^{4}$**	0
β_{17} – TurtleCam 15	0.67	0.1	0.5	0.83	**$8.17 \cdot 10^{7}$**	0
β_{18} – TurtleCam 16	0.61	0.1	0.46	0.77	**$1.14 \cdot 10^{8}$**	0
β_{19} – TurtleCam 18	0.38	0.1	0.22	0.55	**$7.14 \cdot 10^{3}$**	0
β_{20} – TurtleCam 19	0.13	0.1	-0.04	0.3	8.47	37
β_{21} – TurtleCam 20	0.19	0.11	0.02	0.37	26.85	15
β_{22} – TurtleCam 21	-0.48	0.09	-0.63	-0.33	**$1.44 \cdot 10^{-6}$**	0
β_{23} – TurtleCam 22	0.46	0.1	0.3	0.61	**$1.87 \cdot 10^{5}$**	0
β_{24} – TurtleCam 23	-0.33	0.1	-0.49	-0.18	**$3.08 \cdot 10^{-4}$**	0
β_{25} – TurtleCam 24	0.57	0.1	0.41	0.72	**$1.41 \cdot 10^{6}$**	0
β_{26} – TurtleCam 25	0.38	0.1	0.22	0.54	**$5.71 \cdot 10^{3}$**	0
β_{27} – TurtleCam 26	1.05	0.1	0.89	1.21	**$2.79 \cdot 10^{12}$**	0
β_{28} – TurtleCam 27	0.72	0.1	0.57	0.88	**$1.04 \cdot 10^{9}$**	0
β_{29} – TurtleCam 28	0.15	0.1	-0.004	0.31	16.28	27
β_{30} – TurtleCam 29	-0.16	0.1	-0.32	-0.01	0.05	23
β_{31} – TurtleCam 30	-0.38	0.09	-0.53	-0.24	**$5.08 \cdot 10^{-5}$**	0
β_{32} – TurtleCam 31	-0.41	0.09	-0.56	-0.27	**$6.71 \cdot 10^{-6}$**	0
β_{33} – TurtleCam 32	-0.74	0.09	-0.89	-0.59	**$6.46 \cdot 10^{-11}$**	0
β_{34} – TurtleCam 33	-0.77	0.1	-0.93	-0.61	**$2.89 \cdot 10^{-10}$**	0
β_{35} – TurtleCam 34	-0.37	0.1	-0.53	-0.22	**$1.22 \cdot 10^{-4}$**	0
β_{36} – TurtleCam 35	-0.29	0.1	-0.46	-0.12	**0.003**	0
β_{37} – TurtleCam 36	-0.48	0.11	-0.65	-0.31	**$1.03 \cdot 10^{-5}$**	0
β_{38} – TurtleCam 37	-0.17	0.1	-0.34	-0.01	0.043	19
β_{39} – TurtleCam 38	-0.39	0.12	-0.58	-0.2	**$7.16 \cdot 10^{-4}$**	0
β_{40} – TurtleCam 39	-1.12	0.11	-1.29	-0.95	**$1.50 \cdot 10^{-13}$**	0
β_{41} – TurtleCam 40	-0.91	0.11	-1.08	-0.73	**$4.82 \cdot 10^{-10}$**	0

Continued

β_{42} – TurtleCam 41	-0.11	0.1	-0.27	0.05	0.16	46
β_{43} – TurtleCam 42	-0.36	0.1	-0.52	-0.2	**$1.65 \cdot 10^{-4}$**	0
β_{44} – TurtleCam 43	-0.44	0.11	-0.62	-0.27	**$6.80 \cdot 10^{-5}$**	0
β_{45} – TurtleCam 44	-0.92	0.1	-1.09	-0.75	**$3.37 \cdot 10^{-10}$**	0
β_{46} – TurtleCam 45	-0.6	0.09	-0.75	-0.45	**$8.20 \cdot 10^{-9}$**	0
β_{47} – TurtleCam 47	-0.68	0.1	-0.84	-0.52	**$8.81 \cdot 10^{-8}$**	0
β_{48} – TurtleCam 48	-0.41	0.11	-0.59	-0.23	**$2.29 \cdot 10^{-4}$**	0
β_{49} – TurtleCam 49	-0.13	0.1	-0.29	0.03	0.113	38
β_{50} – TurtleCam 50	-0.21	0.1	-0.37	-0.06	0.014	8
β_{51} – TurtleCam 52	-0.05	0.1	-0.21	0.11	0.452	69
β_{52} – TurtleCam 53	0.85	0.11	0.67	1.03	**$3.22 \cdot 10^{8}$**	0
β_{53} – TurtleCam 54	-0.16	0.09	-0.31	-0.01	0.046	24
β_{54} – TurtleCam 58	-0.77	0.09	-0.92	-0.63	**$2.27 \cdot 10^{-11}$**	0
β_{55} – TurtleCam 59	-0.55	0.1	-0.7	-0.39	**$1.51 \cdot 10^{-6}$**	0
β_{56} – TurtleCam 60	0.78	0.1	0.62	0.94	**$2.09 \cdot 10^{8}$**	0
β_{57} – TurtleCam 61	0.77	0.1	0.62	0.92	**$8.44 \cdot 10^{7}$**	0
β_{58} – TurtleCam 62	-0.18	0.1	-0.34	-0.02	0.04	18
β_{59} – TurtleCam 63	2.38	0.17	2.12	2.66	**$3.26 \cdot 10^{17}$**	0
β_{60} – TurtleCam 64	0.23	0.1	0.08	0.39	119.06	3
β_{61} – TurtleCam 65	0.7	0.12	0.5	0.9	**$1.51 \cdot 10^{6}$**	0
β_{62} – TurtleCam 66	0.59	0.12	0.39	0.79	**$3.12 \cdot 10^{5}$**	0

The coefficients for the different 58 TurtleCam IDs from the dive behavior model are presented in Table S3.

Table S3. Coefficients of the random effects from the Dirichlet model, with standard error (SE), 89% Credible Intervals (CI), Bayes Factors (BF), and the percentage of the HDI in the Range of Practical Equivalence (%HDI in ROPE). Note that CI and HDI values are identical, but the original terminology is maintained. BF values between 3.2-10 constitute “Substantial” evidence in favor of the alternative hypothesis H_1 (i.e., positive effect) while values > 10 indicate “Strong” evidence (Kass & Raftery, 1995). The respective ranges in favor of the complementary alternative hypothesis H_{-1} (i.e., negative effect) are 0.3-0.1 and < 0.1. BF values ranging from 0.3 to 3.2 are considered trivial against the null hypothesis H_0 (i.e., no effect). % HDI in ROPE other than 0 indicates “non-decisive” evidence (Kruschke, 2018).

Model Parameter	**Estimate**	**SE**	**5.5% CI**	**94.5% CI**	**BF**	**%HDI in ROPE**
β_4 – TurtleCam 2 - Active	-0.001	0.001	-0.003	0.001	0.285	100
β_5 – TurtleCam 2 – Resting	0.009	0.002	0.007	0.013	$1.37 \cdot 10^{6}$	100
β_6 – TurtleCam 3 – Active	0.002	0.001	$1.36 \cdot 10^{-4}$	0.003	22.84	100
β_7 – TurtleCam 3 – Resting	0.001	0.001	-0.001	0.003	3.15	100

Continued

β_8 – TurtleCam 5 – Active	-0.001	0.001	-0.003	0.001	0.387	100
β_9 – TurtleCam 5 – Resting	0.008	0.002	0.006	0.017	$2.27 \cdot 10^{6}$	100
β_{10} – TurtleCam 6 – Active	-0.008	0.001	-0.009	-0.005	$6.62 \cdot 10^{-8}$	100
β_{11} – TurtleCam 6 – Resting	-0.016	0.002	-0.019	-0.014	$1.01 \cdot 10^{-13}$	100
β_{12} – TurtleCam 7 – Active	-0.001	0.001	-0.002	0.001	0.387	100
β_{13} – TurtleCam 7 – Resting	0.002	0.002	$-1.13 \cdot 10^{-4}$	0.005	14.25	100
β_{14} – TurtleCam 8 – Active	0.004	0.001	0.002	0.005	$1.57 \cdot 10^{4}$	100
β_{15} – TurtleCam 8 – Resting	-0.005	0.002	-0.008	-0.002	0.002	100
β_{16} – TurtleCam 9 – Active	0.002	0.001	$-4.76 \cdot 10^{-5}$	0.004	15.32	100
β_{17} – TurtleCam 9 – Resting	-0.003	0.002	-0.006	$3.56 \cdot 10^{-4}$	0.083	100
β_{18} – TurtleCam 10 – Active	0.001	0.001	-0.001	0.003	3.92	100
β_{19} – TurtleCam 10 – Resting	0.005	0.002	0.002	0.008	278.91	100
β_{20} – TurtleCam 11 – Active	$1.66 \cdot 10^{-4}$	0.002	-0.003	0.004	1.10	100
β_{21} – TurtleCam 11 – Resting	-0.004	0.004	-0.009	0.002	0.182	100
β_{22} – TurtleCam 12 – Active	0.003	0.001	0.002	0.005	0.005	100
β_{23} – TurtleCam 12 – Resting	-0.003	0.001	-0.005	-0.005	0.027	100
β_{24} – TurtleCam 13 – Active	$-1.91 \cdot 10^{-5}$	0.002	-0.002	0.003	0.946	100
β_{25} – TurtleCam 13 – Resting	0.006	0.002	0.003	0.009	536.30	100
β_{26} – TurtleCam 14 – Active	0.003	0.001	0.001	0.004	$1.46 \cdot 10^{3}$	100
β_{27} – TurtleCam 14 – Resting	-0.002	0.001	-0.004	$9.42 \cdot 10^{-5}$	0.068	100
β_{28} – TurtleCam 15 – Active	0.001	0.001	-0.001	0.002	5.29	100
β_{29} – TurtleCam 15 – Resting	-0.001	0.001	-0.003	0.001	0.285	100
β_{30} – TurtleCam 16 – Active	0.001	0.001	-0.001	0.003	3.32	100
β_{31} – TurtleCam 16 – Resting	-0.005	0.002	-0.008	-0.002	0.007	100
β_{32} – TurtleCam 18 – Active	0.001	0.002	-0.001	0.003	3.02	100
β_{33} – TurtleCam 18 – Resting	0.009	0.003	0.006	0.014	$6.35 \cdot 10^{3}$	100
β_{34} – TurtleCam 19 – Active	0.002	0.001	0.001	0.004	144.41	100
β_{35} – TurtleCam 19 – Resting	-0.001	0.001	-0.003	0.001	0.403	100
β_{36} – TurtleCam 20 – Active	0.001	0.001	$-8.77 \cdot 10^{-5}$	0.003	13.59	100
β_{37} – TurtleCam 20 – Resting	$-3.55 \cdot 10^{-4}$	0.001	-0.002	0.002	0.661	100
β_{38} – TurtleCam 21 – Active	0.001	0.001	-0.001	0.003	3.65	100
β_{39} – TurtleCam 21 – Resting	0.001	0.002	-0.003	0.004	1.66	100
β_{40} – TurtleCam 22 – Active	-0.015	0.002	-0.018	-0.012	$3.43 \cdot 10^{-15}$	100
β_{41} – TurtleCam 22 – Resting	-0.021	0.002	-0.025	-0.018	$5.03 \cdot 10^{-14}$	100

Continued

β_{42} – TurtleCam 23 – Active	0.004	0.001	-0.002	0.002	1.66	100
β_{43} – TurtleCam 23 – Resting	0.004	0.002	0.001	0.006	72.82	100
β_{44} – TurtleCam 24 – Active	$9.69 \cdot 10^{-5}$	0.001	-0.002	0.002	1.07	100
β_{45} – TurtleCam 24 – Resting	0.003	0.002	$1.37 \cdot 10^{-5}$	0.006	17.48	100
β_{46} – TurtleCam 25 – Active	0.003	0.001	0.001	0.004	182.86	100
β_{47} – TurtleCam 25 – Resting	$1.04 \cdot 10^{-4}$	0.002	-0.003	0.003	1.10	100
β_{48} – TurtleCam 26 – Active	0.001	0.001	$-3.66 \cdot 10^{-4}$	0.003	8.06	100
β_{49} – TurtleCam 26 – Resting	-0.005	0.002	-0.007	-0.002	0.003	100
β_{50} – TurtleCam 27 – Active	0.002	0.001	0.001	0.004	56.50	100
β_{51} – TurtleCam 27 – Resting	$3.63 \cdot 10^{-4}$	0.002	-0.003	0.004	1.35	100
β_{52} – TurtleCam 28 – Active	-0.001	0.001	0.003	0.001	0.203	100
β_{53} – TurtleCam 28 – Resting	0.007	0.002	0.005	0.009	$3.18 \cdot 10^{5}$	100
β_{54} – TurtleCam 29 – Active	-0.003	0.001	-0.004	$-2.62 \cdot 10^{-4}$	0.037	100
β_{55} – TurtleCam 29 – Resting	0.016	0.002	0.012	0.019	$1.43 \cdot 10^{9}$	100
β_{56} – TurtleCam 30 – Active	-0.01	0.003	-0.015	-0.006	$-2.11 \cdot 10^{-4}$	100
β_{57} – TurtleCam 30 – Resting	-0.015	0.004	-0.022	-0.001	$3.02 \cdot 10^{-5}$	100
β_{58} – TurtleCam 31 – Active	$-2.51 \cdot 10^{-4}$	0.002	-0.003	0.003	1.22	100
β_{59} – TurtleCam 31 – Resting	0.006	0.003	0.001	0.01	38.23	100
β_{60} – TurtleCam 32 – Active	-0.001	0.002	-0.003	0.002	0.547	100
β_{61} – TurtleCam 32 – Resting	-0.008	0.003	-0.013	-0.004	$6.98 \cdot 10^{-4}$	100
β_{62} – TurtleCam 33 – Active	$4.91 \cdot 10^{-4}$	0.002	-0.002	0.003	1.65	100
β_{63} – TurtleCam 33 – Resting	$-8.32 \cdot 10^{-5}$	0.003	-0.005	0.005	0.994	100
β_{64} – TurtleCam 34 – Active	0.002	0.002	-0.001	0.004	6.11	100
β_{65} – TurtleCam 34 – Resting	0.004	0.003	$-3.17 \cdot 10^{-4}$	0.009	13.90	100
β_{66} – TurtleCam 35 – Active	-0.001	0.001	-0.002	0.001	0.447	100
β_{67} – TurtleCam 35 – Resting	-0.003	0.002	-0.006	$-2.49 \cdot 10^{-4}$	0.044	100
β_{68} – TurtleCam 36 – Active	0.002	0.001	0.001	0.004	66.50	100
β_{69} – TurtleCam 36 – Resting	-0.006	0.002	-0.009	-0.003	0.001	100
β_{70} – TurtleCam 37 – Active	$4.71 \cdot 10^{-4}$	0.001	-0.001	0.002	1.84	100
β_{71} – TurtleCam 37 – Resting	0.007	0.002	0.004	0.010	$2.55 \cdot 10^{4}$	100
β_{72} – TurtleCam 38 – Active	0.001	0.001	-0.001	0.002	2.25	100
β_{73} – TurtleCam 38 – Resting	0.003	0.001	$3.61 \cdot 10^{-4}$	0.005	30.35	100
β_{74} – TurtleCam 39 – Active	0.003	0.001	0.001	0.005	324.65	100
β_{75} – TurtleCam 39 – Resting	-0.003	0.002	-0.007	$5.67 \cdot 10^{-4}$	0.097	100

Continued

β_{76} – TurtleCam 40 – Active	0.001	0.001	$-3.62 \cdot 10^{-4}$	0.003	8.51	100
β_{77} – TurtleCam 40 – Resting	0.005	0.002	0.002	0.008	532.82	100
β_{78} – TurtleCam 41 – Active	-0.002	0.001	-0.005	-0.001	0.01	100
β_{79} – TurtleCam 41 – Resting	-0.008	0.002	-0.001	-0.005	$3.63 \cdot 10^{-5}$	100
β_{80} – TurtleCam 42 – Active	-0.001	0.002	-0.003	0.002	0.397	100
β_{81} – TurtleCam 42 – Resting	0.012	0.003	0.008	0.016	$8.92 \cdot 10^{4}$	100
β_{82} – TurtleCam 43 – Active	0.003	0.001	0.001	0.004	807.80	100
β_{83} – TurtleCam 43 – Resting	-0.002	0.002	-0.005	0.001	0.108	100
β_{84} – TurtleCam 44 – Active	0.001	0.001	-0.001	0.002	2.65	100
β_{85} – TurtleCam 44 – Resting	0.002	0.002	$-1.57 \cdot 10^{-4}$	0.005	13.68	100
β_{86} – TurtleCam 45 – Active	0.001	0.001	$-2.67 \cdot 10^{-4}$	0.003	10.71	100
β_{87} – TurtleCam 45 – Resting	0.002	0.002	-0.001	0.004	7.01	100
β_{88} – TurtleCam 47 – Active	$-4.48 \cdot 10^{-4}$	0.001	-0.002	0.003	1.69	100
β_{89} – TurtleCam 47 – Resting	0.008	0.002	0.005	0.011	$6.75 \cdot 10^{4}$	100
β_{90} – TurtleCam 48 – Active	$5.37 \cdot 10^{-6}$	0.001	-0.002	0.002	0.974	100
β_{91} – TurtleCam 48 – Resting	-0.002	0.002	-0.005	0.001	0.139	100
β_{92} – TurtleCam 49 – Active	-0.003	0.001	-0.005	$-2.76 \cdot 10^{-4}$	0.036	100
β_{93} – TurtleCam 49 – Resting	0.009	0.002	0.007	0.013	$5.65 \cdot 10^{5}$	100
β_{94} – TurtleCam 50 – Active	-0.002	0.002	-0.005	$-2.37 \cdot 10^{-4}$	0.084	100
β_{95} – TurtleCam 50 – Resting	0.018	0.002	0.014	0.022	$1.16 \cdot 10^{10}$	100
β_{96} – TurtleCam 52 – Active	-0.001	0.001	-0.003	0.001	0.197	100
β_{97} – TurtleCam 52 – Resting	-0.001	0.002	-0.004	0.001	0.313	100
β_{98} – TurtleCam 53 – Active	0.002	0.001	$2.66 \cdot 10^{-4}$	0.003	37.01	100
β_{99} – TurtleCam 53 – Resting	-0.002	0.001	-0.004	$-1.09 \cdot 10^{-4}$	0.048	100
β_{100} – TurtleCam 54 – Active	-0.006	0.002	0.009	-0.003	0.001	100
β_{101} – TurtleCam 54 – Resting	-0.015	0.003	-0.019	-0.01	$-4.45 \cdot 10^{-6}$	100
β_{102} – TurtleCam 58 – Active	-0.001	0.001	-0.003	0.002	0.421	100
β_{103} – TurtleCam 58 – Resting	0.004	0.002	0.001	0.007	50.44	100
β_{104} – TurtleCam 59 – Active	0.003	0.001	0.001	0.004	433.34	100
β_{105} – TurtleCam 59 – Resting	-0.005	0.002	-0.008	-0.002	0.003	100
β_{106} – TurtleCam 60 – Active	$1.36 \cdot 10^{-4}$	0.001	-0.002	0.002	1.24	100
β_{107} – TurtleCam 60 – Resting	0.003	0.002	$-2.66 \cdot 10^{-4}$	0.005	12.41	100
β_{108} – TurtleCam 61 – Active	-0.001	0.001	-0.003	0.002	0.508	100
β_{109} – TurtleCam 61 – Resting	-0.007	0.002	-0.011	-0.003	0.001	100

Continued

β_{110} – TurtleCam 62 – Active	0.002	0.001	0.001	0.003	66.57	100
β_{111} – TurtleCam 62 – Resting	0.001	0.002	-0.001	0.004	3.22	100
β_{112} – TurtleCam 63 – Active	-0.001	0.001	-0.002	0.001	0.223	100
β_{113} – TurtleCam 63 – Resting	-0.011	0.001	-0.013	-0.009	$2.42 \cdot 10^{-10}$	100
β_{114} – TurtleCam 64 – Active	-0.002	0.002	-0.001	0.004	5.22	100
β_{115} – TurtleCam 64 – Resting	0.003	0.002	-0.001	0.007	10.13	100
β_{116} – TurtleCam 65 – Active	0.002	0.001	0.001	0.004	471.66	100
β_{117} – TurtleCam 65 – Resting	-0.003	0.001	-0.006	-0.002	0.002	100
β_{118} – TurtleCam 66 – Active	0.003	0.001	0.001	0.004	451.41	100
β_{119} – TurtleCam 66 – Resting	-0.003	0.001	-0.005	$-2.88 \cdot 10^{-4}$	0.039	100

Bayesian model diagnostics – MCMC convergence. For the handling stress model, I used 4 Markov Chain Monte Carlo chains (MCMCs) with 3000 iterations each (i.e., 1000 for warm-up and 2000 for sampling). All six model coefficients (β_0 representing the model's intercept, β_1 representing the time effect, and $\beta_{2\text{-}5}$ representing the iterations between the intercept and time with turtle size) did not show prohibitive convergence problems. All chains are presented in Fig. S1.

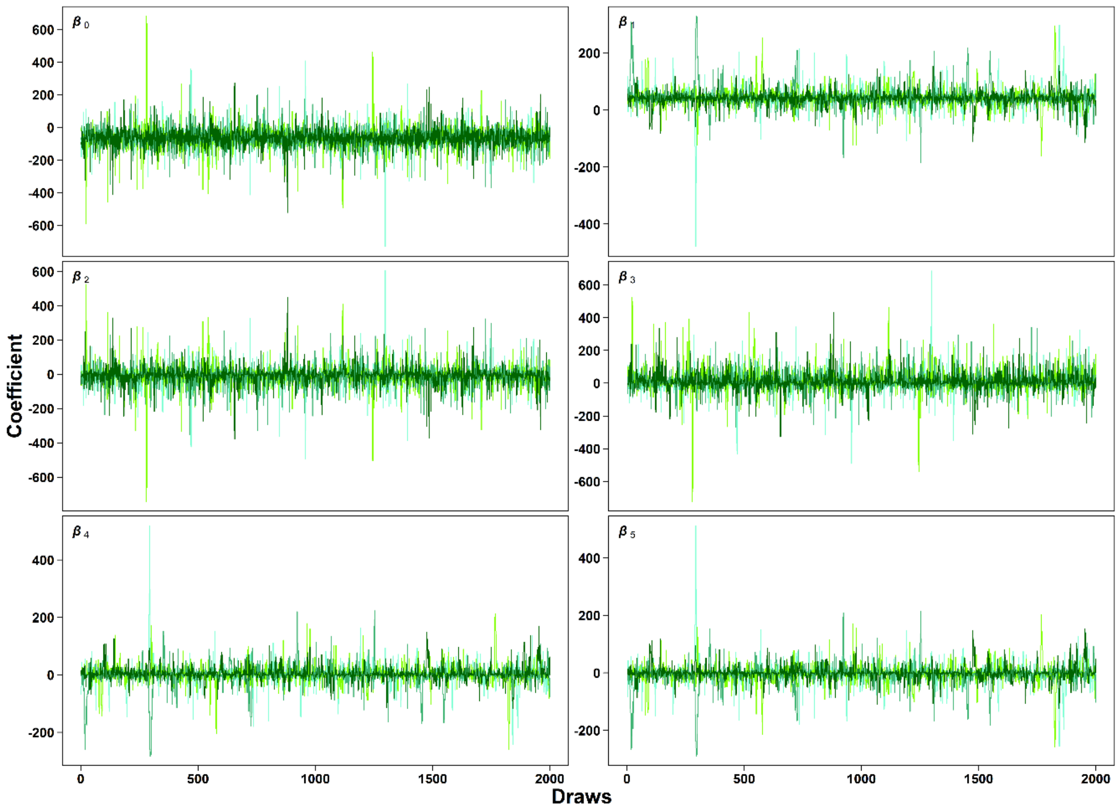

Fig. S1. MCMC trace plot to assess chain convergence after the 2000 sampling iterations (previous 1000 warm-up iterations not shown) for each coefficient of the handling stress model. Each MCMC is represented by a different shade of green.

For the dive variation model, I used 4 Markov Chain Monte Carlo chains (MCMCs) with 12000 iterations each (i.e., 2000 for warm-up and 10000 for sampling). All five model coefficients (β_0 representing the model's intercept, β_1 representing the mean temperature, β_2 representing the maximum dive depth, β_3 representing the effect of time, and β_4 representing the breath duration) did not show prohibitive convergence problems. All chains are presented in Fig. S2.

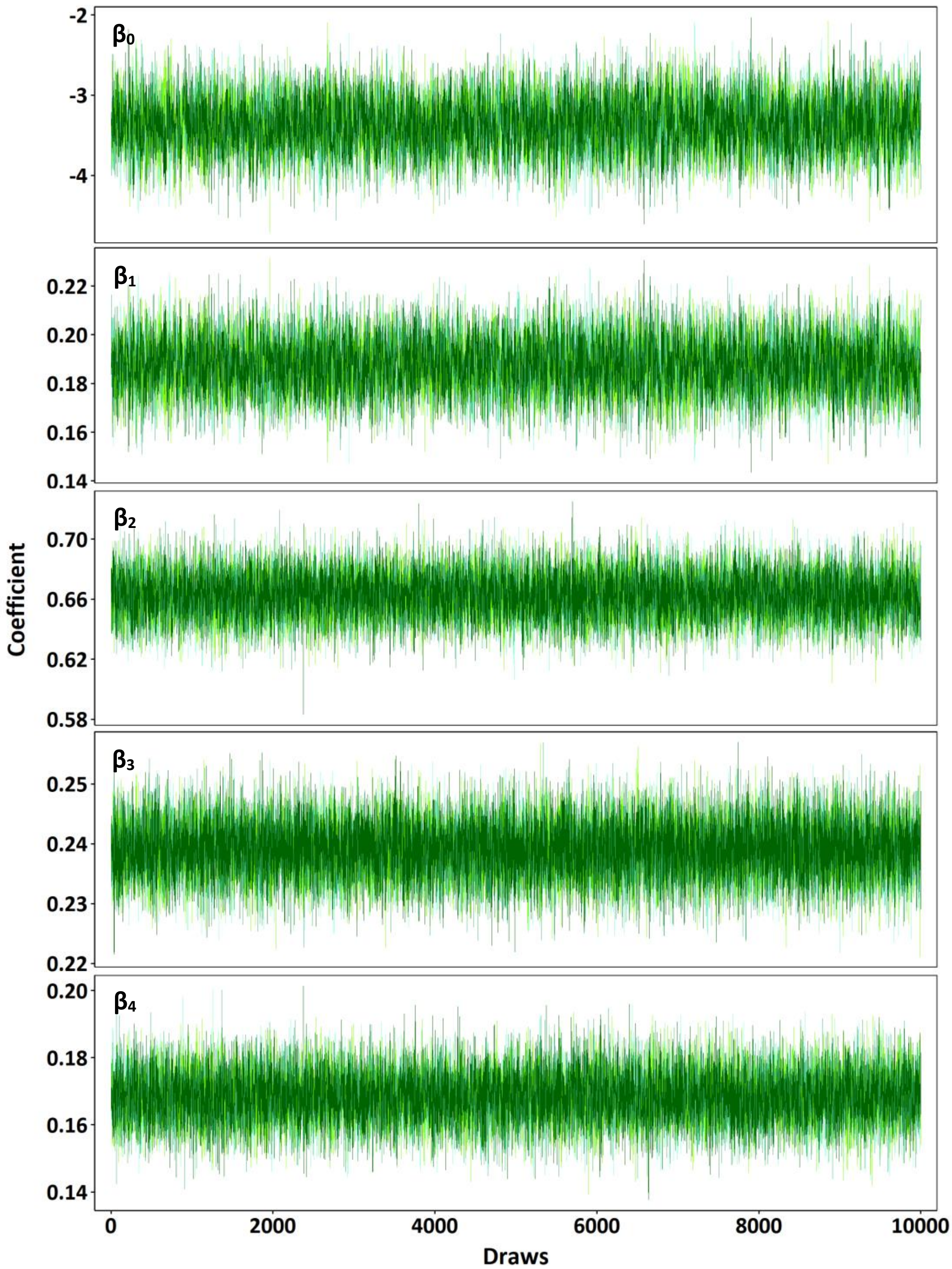

Fig. S2. MCMC trace plot to assess chain convergence after the 10000 sampling iterations (previous 2000 warm-up iterations not shown) for each coefficient of the dive variation model. Each MCMC is represented by a different shade of green.

For the dive behavior model, I used 4 Markov Chain Monte Carlo chains (MCMCs) with 12000 iterations each (i.e., 2000 for warm-up and 10000 for sampling). All four model coefficients (β_0 representing the model's intercept comparing active with feeding behavior, β_1 representing the model's intercept comparing resting and feeding behavior, β_2 representing comparison between active and feeding behavior, and β_3 representing the comparison between resting and feeding behavior) did not show prohibitive convergence problems. All chains are presented in Fig. S3.

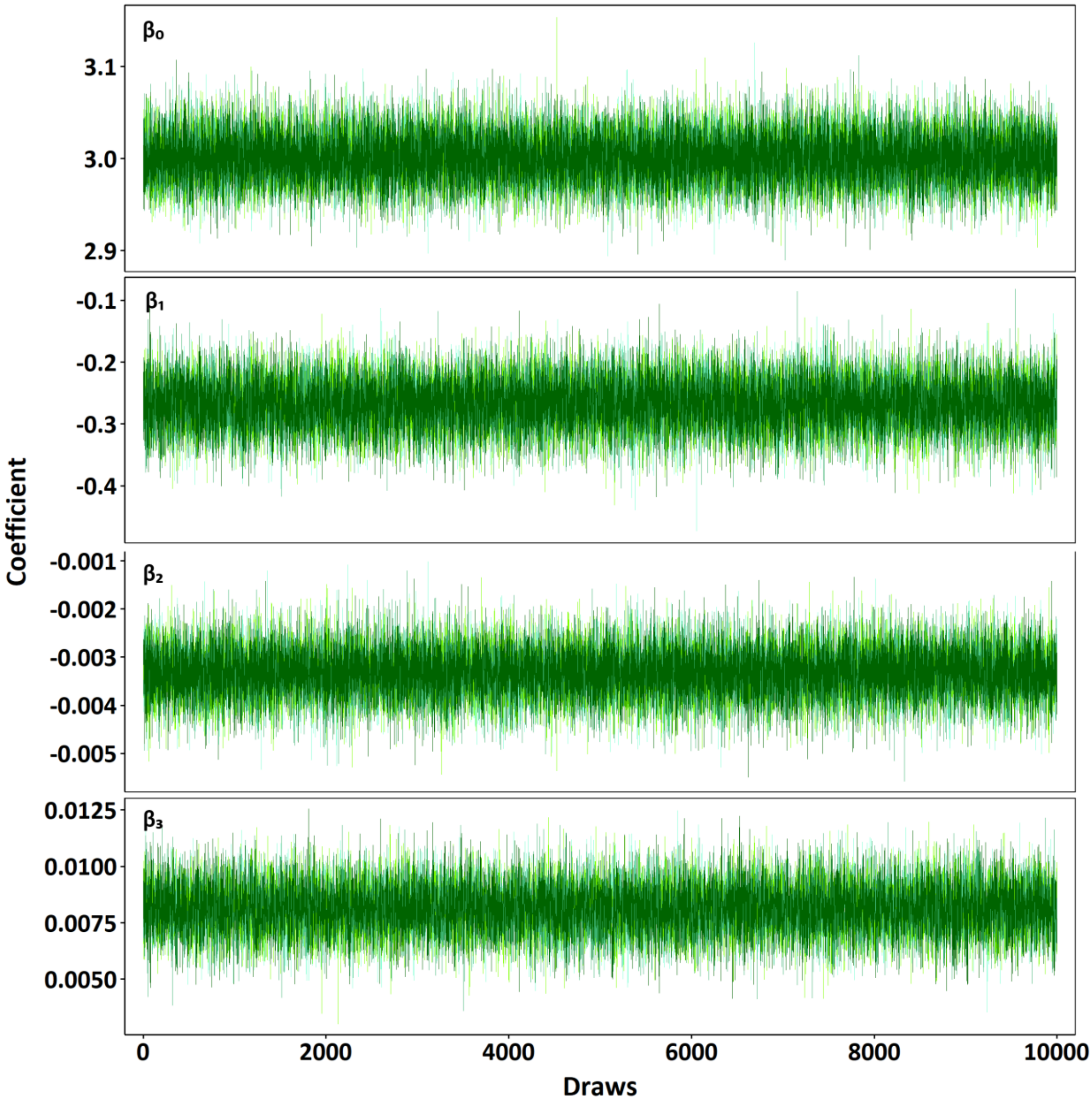

Fig. S3. MCMC trace plot to assess chain convergence after the 10000 sampling iterations (previous 2000 warm-up iterations not shown) for each coefficient of the dive behavior model. Each MCMC is represented by a different shade of green.

Bayesian model output – Posterior distributions. Fig. S4 displays the full posterior distributions (1000 draws) of the handling stress model's coefficients, providing high-resolution insight into the information presented in Fig. 2.4 of the main text. Regarding the effect of time, 0 falls outside the range of the 89% Credible Intervals, indicating the strongest contribution of this parameter to the model's variance.

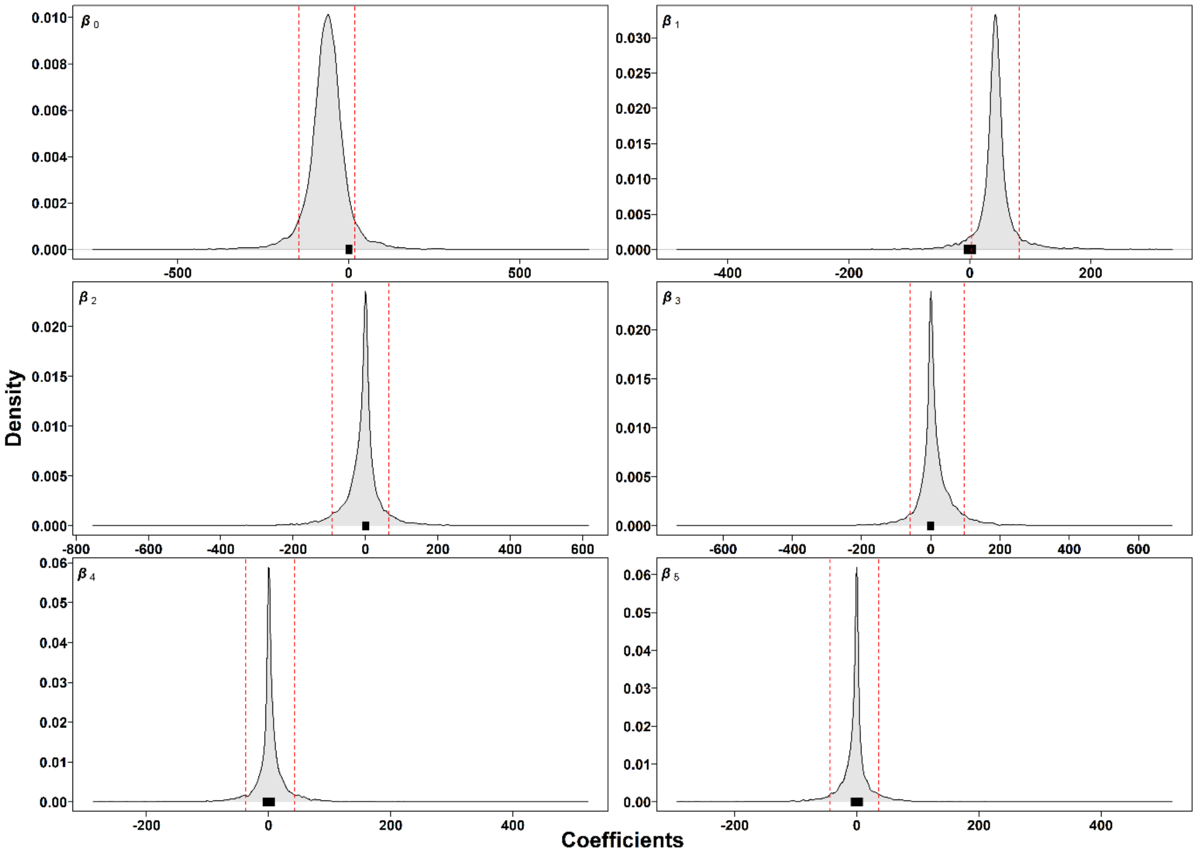

Fig. S4. Posterior distributions of the handling stress model coefficients. Distributions are presented in the form of kernel density plots, where the total area below the curve integrates to 1. The red dashed vertical lines indicate the 89% Credible Intervals. The thick black area around 0 indicates the Region Of Practical Equivalence (ROPE).

Fig. S5 displays the full posterior distributions (1000 draws) of the dive variation model's coefficients, providing high-resolution insight into the information presented in Fig. 2.5 of the main text. In all five coefficients, 0 falls outside the range of the 89% Credible Intervals, with the effect of time being the strongest contribution of this parameter to the model's variance followed by the maximum dive depth, the breath duration, and the mean temperature.

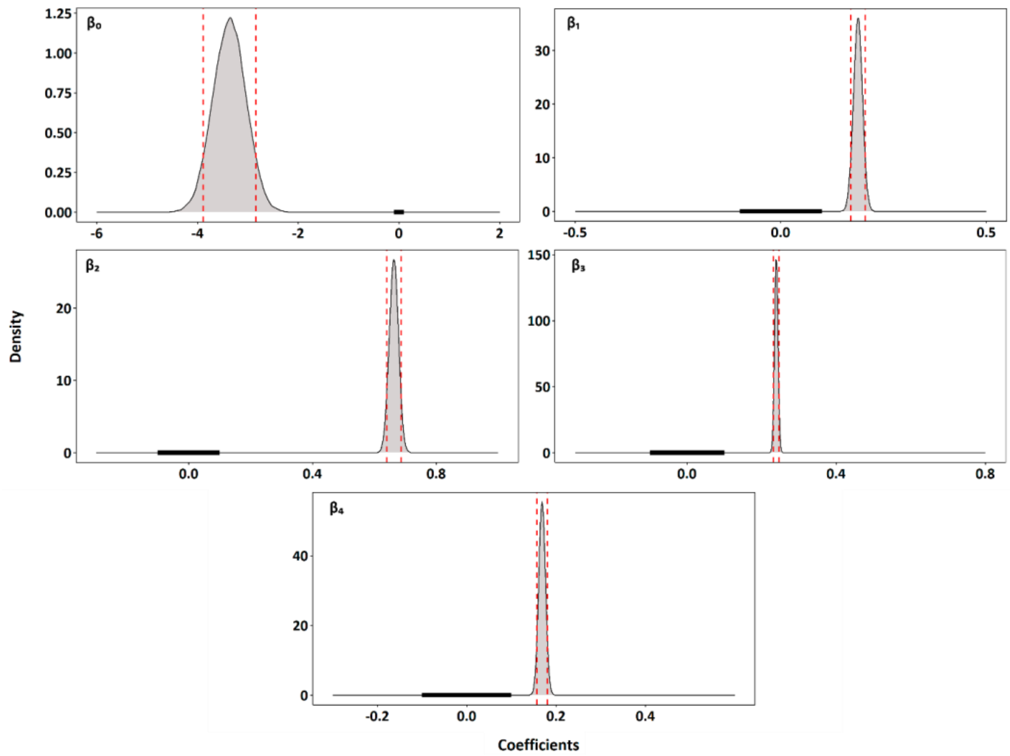

Fig. S5. Posterior distributions of the dive variation model coefficients. Distributions are presented in the form of kernel density plots, where the total area below the curve integrates to 1. The red dashed vertical lines indicate the 89% Credible Intervals. The thick black area around 0 indicates the Region Of Practical Equivalence (ROPE).

Fig. S6 displays the full posterior distributions (1000 draws) of the dive behavior model's coefficients, providing high-resolution insight into the information presented in Fig. 2.9 of the main text. Only the 0 from the intercept comparing active and feeding behavior (β_0) and the intercept comparing resting and feeding behavior (β_1) fall outside the range of the 89% Credible Intervals, with the effect of β_0 being the strongest contribution of this parameter to the model's variance.

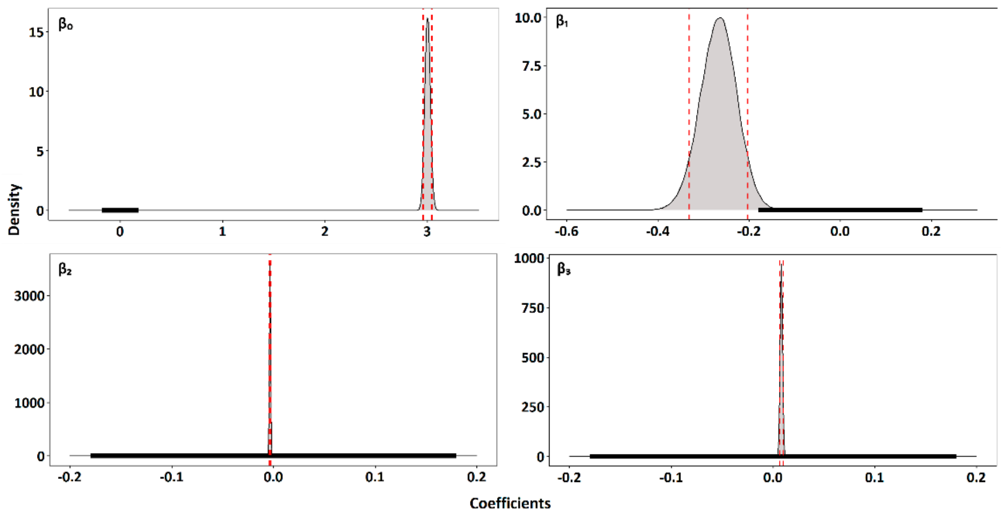

Fig. S6. Posterior distributions of the behavior model coefficients. Distributions are presented in the form of kernel density plots, where the total area below the curve integrates to 1. The red dashed vertical lines indicate the 89% Credible Intervals. The thick black area around 0 indicates the Region Of Practical Equivalence (ROPE).

Change of mean temperature over time since release. Fig. S7 illustrates the fluctuations in mean temperature over time since the deployment of the 58 TurtleCams. Most of the TurtleCams exhibit an increase in mean temperature over time.

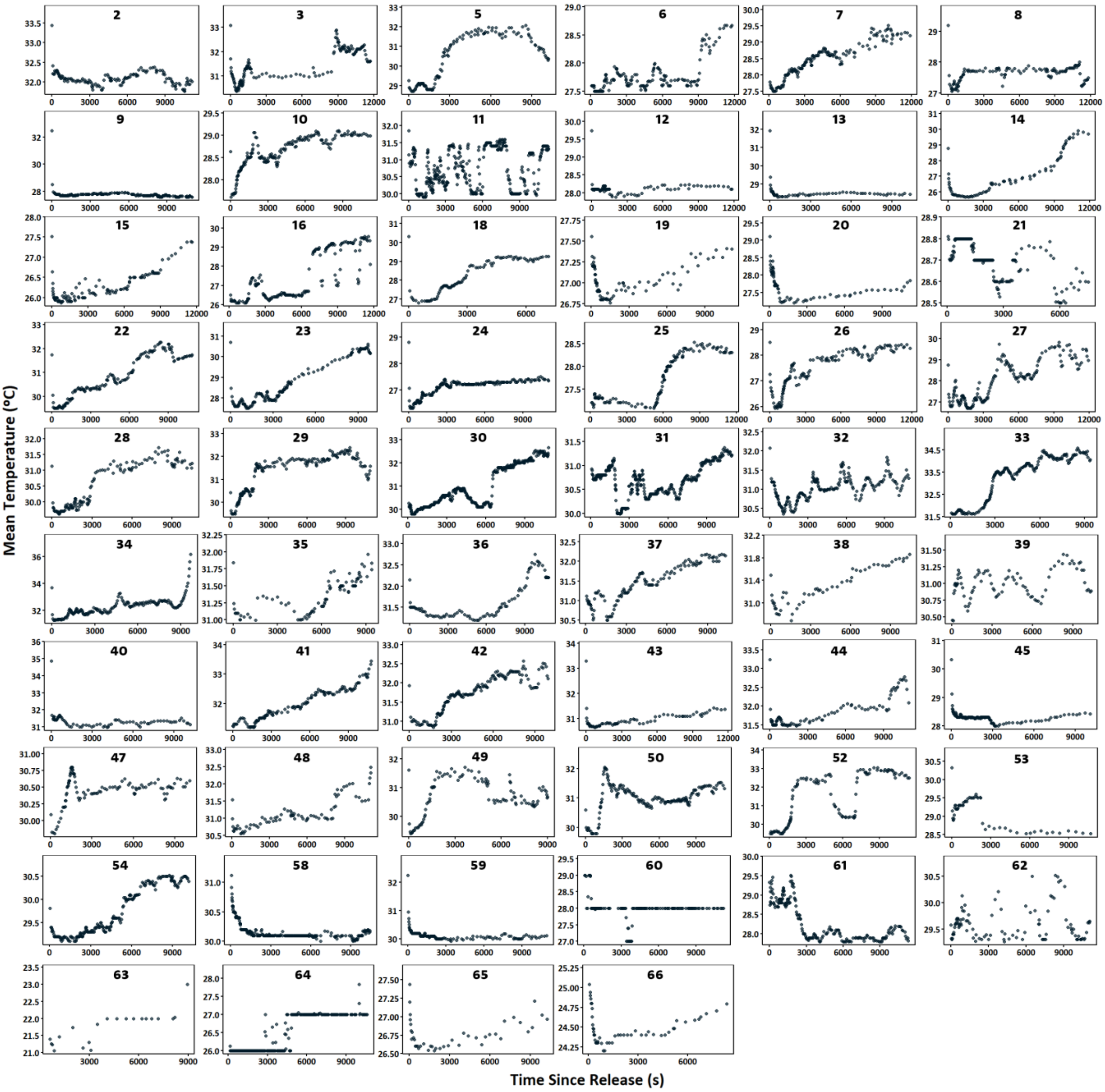

Fig. S7. Changes of the mean temperature over time since the deployment of the TurtleCams. The number at the top of each graph represents the TurtleCam ID.