



Gravid green turtles employ a mixed capital–income breeding strategy where food is abundant

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ABSTRACT: Sea turtles are marine ectotherms commonly considered capital breeders that use accumulated energy stores for reproduction. In some green turtle *Chelonia mydas* populations, gravid females feed during the inter-nesting period, indicating that they are not exclusively capital breeders but may supplement energy stores with energy gained through feeding during inter-nesting periods. However, the significance of this feeding remains unknown, as does the time allocation between energy intake and energy-saving behaviors during inter-nesting periods. In this study, we deployed video, head-mounted acceleration, and GPS loggers on 9 green turtles nesting on Ishigaki Island, Japan, to monitor their feeding behavior during the inter-nesting period. We found that the turtles spent nearly half of the inter-nesting period resting (42.1% on average), but also dedicated 3.4% of their time to foraging, exhibiting a bimodal daily pattern with peaks in activity during the early morning and evening. Most feeding occurred around the algae/seagrass meadows in close vicinity to resting sites, so little energy is required to shuttle between feeding and resting sites. In such cases, the energy stores acquired prior to the breeding migration can be 'topped up' with feeding during inter-nesting intervals. Our results indicate that gravid green turtles employ a mixed capital–income breeding strategy in which females mostly rely on capital energy, but may supplement this with small amounts of income energy gained by feeding during inter-nesting periods.

KEY WORDS: Bio-logging · Capital breeding · *Chelonia mydas* · Income breeding · Inter-nesting period · Grazing · Reproductive strategy · Sea turtle

1. INTRODUCTION

Life history theory deals with how animals allocate resources to maximize fitness (Stearns 1992). Energy

storage is a critical component of life history variation. An aspect of energy storage that has generated particular interest is energy for reproduction (Drent & Daan 1980, Stearns 1992, Jönsson 1997). Energy used

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for reproduction can conceptually be divided between 'income breeders' and 'capital breeders' (sensu Drent & Daan 1980). Capital breeders primarily acquire resources in advance of a reproductive bout and store them until they are required for offspring production, whereas income breeders primarily rely on resources gained during a breeding bout. Based on the theoretical analysis (Jönsson 1997), income breeding is the most advantageous strategy in a perfectly predictable environment without limited resources, as capital breeders may have to face additional energetic costs while accumulating their stored resources. However, capital breeding offers many benefits where there are unpredictable food conditions, food and time limitations, and/or risky foraging conditions (Jönsson 1997).

Theoretical and empirical studies on the evolution of capital versus income breeding need to consider the critical roles of the thermoregulatory and metabolic systems of animals (Bonnet et al. 1998, Shine 2003). Ectotherms are often capital breeders because of much lower metabolic costs associated with ectothermy than with endothermy, so that energy stores are relatively more readily accumulated in ectotherms (Bonnet et al. 1998). Sea turtles are marine ectotherms that are commonly considered capital breeders (Miller 1997). Because they usually migrate long distances from foraging to breeding grounds, their reproduction has been considered to rely on body reserves gained from their foraging grounds (Miller 1997). Particularly for benthic feeders, including green turtles *Chelonia mydas* and hawksbill turtles *Eretmochelys imbricata*, abundant forage is not expected to be available during their pelagic migration from foraging to breeding grounds. Therefore, a capital breeding strategy is presumed advantageous or necessary when a large energy expenditure is required to reach the breeding grounds.

During their breeding period, sea turtles nest several times and may spend several months near nesting sites (Miller 1997, Hays et al. 2002a, Hamann et al. 2003). The period between successive nesting events during a single breeding season is called the inter-nesting period (Miller 1997). Many studies have reported that nesting turtles do not feed during inter-nesting periods, but usually spend most of their time at rest on the sea floor or floating in mid-water to limit their energy expenditure (Carr et al. 1974, Mortimer & Portier 1989, Liew & Chan 1992, Tanaka et al. 1995, Hays et al. 2000, 2002a, Hamann et al. 2002, Plot et al. 2013, Okuyama et al. 2016). Sporadic feeding behaviors during inter-nesting periods have been inferred based on body mass changes and behavioral (diving

and mouth-opening patterns and esophageal temperature) studies in 3 of the 7 sea turtle species (hawksbill turtles: Santos et al. 2010; loggerhead turtles *Caretta caretta*: Houghton et al. 2002, Schofield et al. 2006; and leatherback turtles *Dermodochelys coriacea*: Southwood et al. 2005, Fossette et al. 2008, Casey et al. 2010). However, these studies have concluded that feeding is rare and opportunistic. Reportedly, only green turtles have behavioral plasticity for obtaining energy for reproduction (Hays et al. 2002b): several populations rest and avoid unnecessary energy expenditure in breeding areas where food is unavailable during the inter-nesting period (Carr et al. 1974, Mortimer & Portier 1989, Liew & Chan 1992, Hays et al. 2000, Hamann et al. 2002, Yasuda & Arai 2009), while others feed at sites where abundant forage is available (Balazs 1980, Hochscheid et al. 1999, Tucker & Read 2001, Hays et al. 2002b, Fuller et al. 2009, Stokes et al. 2019). Indeed, Hochscheid et al. (1999) estimated that green turtles nesting in Cyprus forage for 34% of their time during inter-nesting periods. This estimation was based on dive profile and activity level data, but did not use more direct methods for detecting feeding behaviors, such as animal-borne video cameras (but for green turtles: Okuyama et al. 2013; for leatherback turtles: Wallace et al. 2015), mouth-opening sensors (but for leatherback turtles: Fossette et al. 2008), and head-mounted acceleration loggers (but for green turtles: Okuyama et al. 2009, 2013). There is little direct evidence and understanding of whether such feeding is deliberately targeted or only opportunistic, and how time is allocated between energy intake (feeding) and energy saving (resting) behaviors. In this study, opportunistic feeding is defined as unintentional feeding resulting from a situation wherein turtles incidentally encounter food, whereas targeted feeding is a behavior wherein turtles actively search for food and consequently feed on it.

Many sea turtles exhibit a diel pattern in their activity, being active during the day and resting at night (green turtles: Ballorain et al. 2013, Okuyama et al. 2013; hawksbill turtles: van Dam & Diez 1997, Okuyama et al. 2010; loggerhead turtles: Freitas et al. 2018, Fujita et al. 2023; and leatherback turtles: James et al. 2006, Okuyama et al. 2021), suggesting that they are mostly diurnal foragers, but few studies report if there are times during daylight when feeding activity is more intense (Taquet et al. 2006, Okuyama et al. 2013).

In this study, we deployed video cameras, head-mounted accelerometers, and GPS loggers on nesting green turtles to monitor their feeding behavior during the inter-nesting period. Herein, we report how they

engage in targeted feeding and allocate time spent on feeding and resting behaviors during their inter-nesting period.

2. MATERIALS AND METHODS

2.1. Tag deployment

This study was conducted during the green turtle nesting season (July and August) in 2009, 2010, 2013, and 2022 at Ibaruma Beach, Ishigaki Island, Japan (24.528° N, 124.298° E). Ishigaki Island is a nesting site for green, loggerhead, and hawksbill turtles (Okuyama et al. 2020). Sunrise and sunset times on Ishigaki Island during the research period fell between 06:00 and 06:13 h, and between 19:25 and 19:36 h, respectively. We deployed various types of tags on 9 green turtles (Table 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m764p175_supp/). These tags included head- and body-mounted multi-sensor data loggers, a Fast-loc GPS logger, and a custom-made video logger with a scheduled recording system and extra battery in a waterproof case (see Table S1 for details of tag manufacturers, equipped sensors, dimensions, and sampling rates). Videos were recorded for 10 min every 3 h starting at 06:30, 09:30, 12:30, 15:30, and 18:30 h from the second day of the inter-nesting period. The video recording lasted for 3–4 d because of battery exhaustion. The other tags recorded the behavior of each turtle during the entire inter-nesting period, except for the head-mounted acceleration logger for ID 4, which was

recorded for only 72 h in the middle of the inter-nesting period because of the limitation of data storage (Table 1). We synchronized the clocks of all loggers used in this study before deployment. As both head- and body-mounted multi-sensor data loggers were equipped with depth sensors, their clocks were synchronized based on the depth profile. When the turtles were deployed with the GPS loggers, the clocks of all loggers deployed were synchronized with reference to that of the GPS logger. When a turtle surfaced for breathing, the GPS fixed its location. Based on the depth profile of the turtle while surfacing, the clocks of the head- and body-mounted loggers and the GPS logger were synchronized. Similarly, the time points of the video data and those of the data from the other loggers were synchronized as the surfacing and breathing behaviors were recorded by the video camera logger.

We patrolled the nesting beaches nightly to find the turtles. After oviposition, we measured the straight carapace length and body weight, cleaned the carapace with sandpaper, and securely attached the tags to the carapace or head using epoxy resin and fiberglass cloth (Konishi). This deployment protocol was a modification of the protocol described by Okuyama et al. (2013). After the resin had completely dried, the turtles were released into the sea. Within 9–10 d after deployment, the turtles re-emerged on the same beach for nesting. The tags were then retrieved using a metallic spatula and rubber hammer.

While the behavior of IDs 1 and 3 was being recorded, Typhoon Soulik passed across Ishigaki Island, causing heavy rain, strong winds, and turbulence in

Table 1. Summary of physical data, tag deployment period, and sensors deployed for the green turtles used in this study. SCL: straight carapace length; BW: body weight; D: depth; T: temperature; BA: body acceleration; HA: head acceleration; G: GPS; V: video; fps: frames per second

Turtle ID	SCL (cm)	BW (kg)	Tag deployment period	Sensors and sampling rate
1	94.6	–	7–16 July 2013	D (1 Hz), T (1 Hz), BA (8 Hz), HA (15 Hz), G (5 min while surfacing), V (30 fps)
2	97.5	120	21–30 July 2013	D (1 Hz), T (1 Hz), BA (8 Hz), HA (15 Hz), G (5 min while surfacing), V (30 fps)
3	107.4	–	9–19 July 2013	D (1 Hz), T (1 Hz), BA (8 Hz), HA (15 Hz), V (30 fps)
4	100.9	130	19–29 July 2009	D (1 Hz), T (1 Hz), BA (8 Hz), HA (32 Hz) ^a
5	99.1	–	4–13 July 2022	D (1 Hz), T (1 Hz), HA (8 Hz)
6	95.5	123	16–24 July 2010	D (1 Hz), T (1 Hz), BA (8 Hz), G (5 min while surfacing)
7	100.2	128	17–25 July 2010	D (1 Hz), T (1 Hz), BA (8 Hz), G (5 min while surfacing)
8	94.8	132	29 July to 6 August 2010	D (1 Hz), T (1 Hz), BA (8 Hz), G (5 min while surfacing)
9	109.0	153	31 July to 10 August 2010	D (1 Hz), T (1 Hz), BA (8 Hz), G (5 min while surfacing)

^aHA for ID 4 was recorded for only 72 h (24–26 July 2009)

the sea around Ishigaki Island from 11 to 13 July 2013. Therefore, we investigated the effects of this typhoon on the behavior of these 2 turtles.

2.2. Data analysis

2.2.1. Video analysis

Video data were analyzed to count the feeding events and determine the timing, depth, and horizontal location when feeding events occurred. Three feeding behavior patterns were identified: benthic feeding on algae on the substrate, midwater feeding on seagrass/algae or jellyfish drifting in the water column, and surface feeding on floating seagrass (Fig. 1; Videos S1–S3 in the Supplement at www.int-res.com/articles/suppl/m764p175_supp/). Differences in the number of feeding events for these 3 patterns in the 5 recording time slots were tested using a χ^2 test. This statistical analysis was performed using R (v. 4.4.2; R Core Team 2021). Moreover, as many food items as possible were identified in the video footage.

2.2.2. Identifying feeding events and behavioral patterns based on head acceleration and depth data

To investigate feeding behavior during the period when video footage was not available, feeding events were extracted from the head acceleration and depth data following the extraction procedure described by Okuyama et al. (2009, 2013). The obtained time-series data were analyzed using IGOR Pro software (WaveMetrics) and Ethographer (Sakamoto et al. 2009). First, we established the extraction conditions for feeding events from 3 turtles (IDs 1–3), where both video and head acceleration were simultaneously recorded. Acceleration sensors measure both dynamic (e.g. flipper movement and head motion) and static (e.g. posture) accelerations, represented as high- and low-frequency components, respectively (Okuyama et al. 2009). We

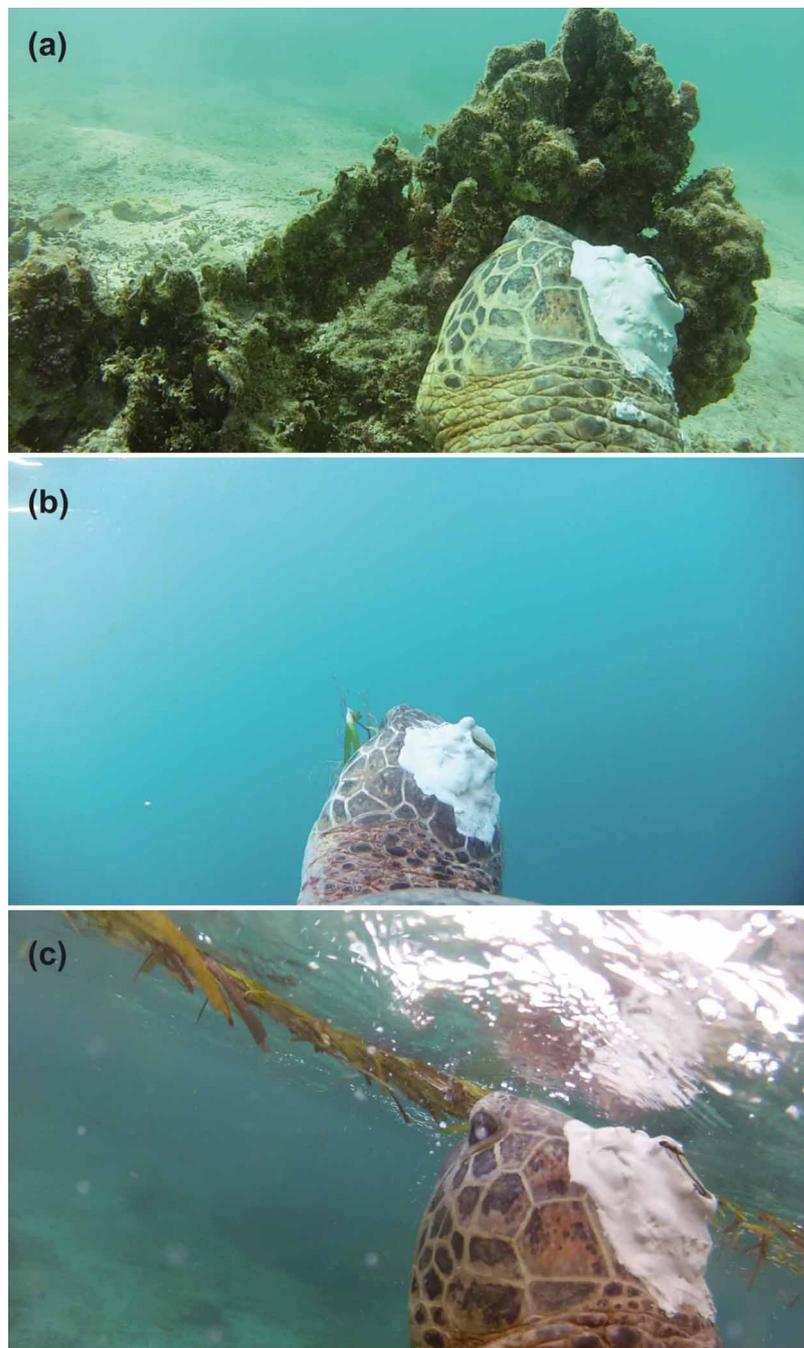


Fig. 1. Three patterns of green turtle feeding behavior recorded by animal-borne video cameras mounted on the carapace. The white mass visible on the turtle's head is epoxy putty used to attach the data logger. (a) Benthic feeding (grazing) on food on the substrate, (b) midwater feeding on food within the water column, and (c) surface feeding on seagrass floating at the surface. Video footage corresponding to these images is available in Videos S1–S3 in the Supplement

separated the head acceleration components in the surging and swaying axes into each dynamic motion and posture using a 0.32 Hz low-pass filter using the IGOR Filtering Design Laboratory software (Wave-

Metrics) based on the value defined by Okuyama et al. (2009). Based on the acceleration values of the dynamic component of head acceleration in surging and swaying axes and depth data when a feeding bite was observed by the video logger, 3 feeding patterns were defined as follows: benthic feeding on the substrate (seafloor, coral rubble, and rock) that consisted of 0.1 to 0.35 *g* or -0.35 to -0.1 *g* in surging acceleration and >0.12 *g* or <-0.12 *g* in swaying acceleration in the head motion while diving; midwater feeding that comprised 0.12 to 0.2 *g* or -0.2 to -0.12 *g* in surging acceleration and 0.04 to 0.08 *g* or -0.08 to -0.04 *g* in swaying acceleration while diving; and surface feeding that was defined as 0.1 to 0.25 *g* or -0.25 to -0.1 *g* in surging acceleration and >0.12 *g* or <-0.12 *g* in swaying acceleration when the turtle was at a depth shallower than 0.5 m. Dives were defined as events exceeding 0.5 m in depth for at least 30 s, and dive parameters were extracted for each dive. Consecutive feeding signals within 5 s were considered a single feeding event (Okuyama et al. 2009). Feeding signals lasting <1 s were removed to eliminate noise from contact with obstacles (e.g. rocks). Under these conditions, we extracted feeding events based on head acceleration and depth data. Subsequently, we calculated the detection and false detection rates of events by comparing the numbers of feeding events extracted based on head acceleration and depth data and video observations in 3 turtles (IDs 1–3). The detection rate was almost perfect (98.6%; 73 of 74), whereas the false detection rate was 5.4% (10 of 185). Although we employed various sampling rates (8–32 Hz) of head acceleration data to detect feeding events in this study, the values for the detection and false detection rates did not change across the different sampling rates. This was verified by comparing the detection and false detection rates of feeding events observed in 3 turtles (IDs 1–3) extracted by original sampling rate (15 Hz) and the resampled rate of 8 Hz. Resampling was conducted using the resampling function in IGOR Pro. This extraction condition for feeding events from the head acceleration and depth data was then applied to 5 turtles equipped with head-mounted accelerometers to detect their feeding events (IDs 1–5).

To understand how turtles spent time during the inter-nesting period, their behavioral patterns were classified into the following 7 types: benthic feeding, midwater feeding, surface feeding, bottom resting, midwater resting, surfacing, and 'other behaviors,' based on dive and head-acceleration profiles, and feeding events. The durations of benthic, midwater, and surface feeding behaviors were defined as the time periods during which events of each feeding type were extracted.

Bottom resting behavior was defined as a behavior occurring when the following conditions were met for more than 10 s: the change in depth every 1 s was <0.15 m, and the average change per second in the absolute dynamic head acceleration in the surging axis was <0.005 *g*. Similarly, midwater resting behavior was defined as meeting the following conditions during a gradual ascent phase (cf. Type 3 and Type 4, Minamikawa et al. 1997, Wilson et al. 2017): the change in depth every 1 s was <0.15 m and the average change per second in the absolute dynamic head acceleration in the surging axis was <0.1 *g* (see Fig. S1 for the depth and body/head acceleration profiles while midwater resting, and Video S4 for footage during this type of dive). Surfacing behavior was defined as turtles staying at a depth shallower than 0.5 m, except for surface feeding behavior. 'Other behaviors' included the duration of all behaviors, except feeding and resting. The time spent on each behavior type was then calculated. Moreover, we investigated the change in the time proportion as the inter-nesting period progressed. However, for this analysis, we removed the data for the days when the typhoon passed through Ishigaki Island, because the behavioral patterns of the turtles were presumably affected by this typhoon. In our study, the turtles returned to the sea between midnight and dawn after tag deployment. If the turtles returned to the sea before midnight, the following day was defined as the first day; otherwise, if they returned after midnight, that day was considered the first day. Individual differences in time allocation (feeding, resting, surfacing, etc.) were tested using the χ^2 test function from the standard R package (R Core Team 2021).

2.2.3. Horizontal movement data analyses

GPS data were analyzed using R (R Core Team) and QGIS (QGIS Development Team) software. To remove erroneous locations, we employed the Fast-loc location filter suggested by Dujon et al. (2014), using only location data with more than 4 GPS satellites and a residual value of <35 . In addition, data were removed when a location occurred on land. To investigate the movement and changes in habitat use by turtles during the inter-nesting period, the daily location center was calculated by averaging the latitude and longitude coordinates for each day. We estimated individual home ranges using 95% fixed kernel (FK) and 50% FK isopleths for each of 6 individuals (IDs 1, 2, 6–9; Table 1) using the R package 'adehabitatHR' (Calenge 2011). Distribution data for coral reefs and dense seagrass/seaweed beds around Ishigaki Island were obtained

from the GIS data set available from the Biodiversity Center of Japan, Ministry of the Environment, based on the Fourth National Basic Survey on the Natural Environment (Biodiversity Center of Japan, Ministry of the Environment 2021). Distribution data for dense seagrass and seaweed beds were created based on satellite images captured in 1999 and 2018, respectively. Thus, seagrass and seaweed distributions only represent areas with dense growth, and not those with scattered patches.

To determine habitat use by turtles during the inter-nesting period, the relationship between the location and behavioral patterns of the turtles was investigated. As the location data were fixed while surfacing, the behavioral pattern at a given location was defined as the behavioral pattern during the subsequent dive, except for surface feeding. Benthic and midwater feeding locations were defined as given locations followed by dives incorporating at least a single event of benthic and midwater feeding, respectively. When surface feeding was observed at a given location, the behavioral pattern was defined as 'surface feeding'. Bottom resting locations were defined as given locations followed by a dive with >80% bottom resting behavior during the bottom phase. In contrast, midwater resting locations were defined as given locations followed by a dive with >80% midwater resting behavior during the gradual ascent phase. The locations of 'other behaviors' were defined as locations other than those used for feeding and resting behaviors. Furthermore, the core and usual areas of the locations where the turtles engaged in benthic feeding and bottom resting were calculated using the FK density estimation. The core and usual areas were defined as the 50 and 95% FK isopleths, respectively, for each behavior.

3. RESULTS

3.1. Feeding behavior recorded by video loggers

The video camera recorded the behavior of 3 turtles (IDs 1–3) for 130, 200, and 200 min, respectively, during the inter-nesting period. Feeding behavior was observed for all 3 turtles. Three feeding behavior patterns were identified: benthic feeding on algae on the substrate, midwater feeding on seagrass/algae or jellyfish drifting in the water column, and surface feeding on floating seagrass (Fig. 1; Videos S1–S3). During the video recording period, 729 feeding events were observed for the 3 turtles (Fig. 2). Of these, 608, 45, and 76 were benthic, midwater, and

surface feeding events, with average durations (\pm SD) of 92.1 ± 128.8 , 13.9 ± 9.7 , and 45.5 ± 83.4 s, respectively. Feeding events per turtle were particularly concentrated between 06:30 and 06:40 h and between 18:30 and 18:40 h (Fig. 2). The proportions of the 3 feeding patterns were significantly different across the recording time slots (χ^2 test, $df = 8$, $\chi^2 = 38.1$, $p < 0.001$). For example, benthic feeding events were observed only in the morning and evening (06:30–06:40, 09:30–09:40, and 18:30–18:40 h), and no events were observed in the afternoon (12:30–12:40 and 15:30–15:40 h). Midwater feeding events occurred throughout most of the recorded time slots, whereas surface feeding events were observed only in the morning and evening (06:30–06:40 and 18:30–18:40 h). The depths where the events of benthic, midwater, and surface feedings occurred were 3.7 ± 5.0 , 7.9 ± 3.7 , and 0.4 ± 0.2 m, respectively. Video analyses revealed that the turtles mainly feed on the rhodophyte *Digenea simplex* ($N = 277$), certain species of red algae ($N = 245$), brown algae (*Dictyota* spp., $N = 12$), unidentified algae ($N = 50$), seagrasses (*Thalassia hemprichii*, *Cymodocea rotundata*, *C. serrulata*, $N = 94$), jellyfish ('unidentified species', $N = 2$), a plastic bag ($N = 1$; Video S5), and unidentified food ($N = 48$).

3.2. Extraction of feeding behavior by linking video with depth and head acceleration data

A total of 10 440 feeding events were extracted from the head acceleration and depth data during the inter-nesting period for 5 turtles (IDs 1–5) based on

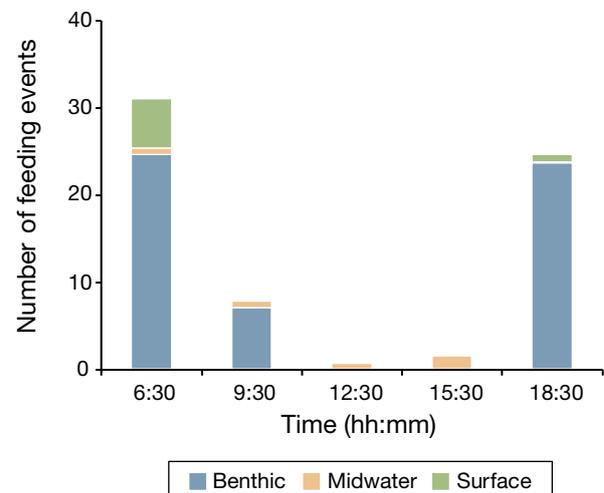


Fig. 2. Mean number of the 3 different types of feeding events recorded using video loggers at recording time slots (10 min) for 3 gravid green turtles (IDs 1–3) during their inter-nesting period

the extraction conditions (Fig. 3). Of these events, the proportion (mean \pm SD) of benthic feeding was $74.1 \pm 17.3\%$, whereas those of midwater and surface feeding were 18.1 ± 15.0 and $7.8 \pm 2.5\%$, respectively. The durations of each feeding event were 12.6 ± 12.6 s for benthic ($N = 8096$), 8.5 ± 7.6 s for midwater ($N = 1608$), and 8.4 ± 8.0 s for surface feeding ($N = 736$), respectively. The mean depths (\pm SD) of feeding events were 2.86 ± 0.95 m for benthic, 4.12 ± 1.70 m for midwater, and 0.48 ± 0.18 m for surface feeding events.

Similar to the video observations of feeding events, the timing of feeding events extracted from the head acceleration and depth data showed bimodal peaks during the day and were concentrated around 06:00 and 18:00 h (Fig. 4). The diel pattern of benthic feeding showed bimodal peaks during the day, as opposed to surface and midwater feeding, which did not show any diel pattern (Fig. 4).

3.3. Ethogram of green turtles during their inter-nesting period

The 4 turtles (IDs 1–3, 5) for which the behavioral patterns were recorded during the entire inter-nesting period spent the inter-nesting period engaged in all

3 types of feeding (mean \pm SD: $3.44 \pm 1.16\%$), resting ($42.1 \pm 18.7\%$), other activities ($49.4 \pm 19.2\%$), and surfacing behaviors ($5.1 \pm 1.9\%$). However, the time spent on each behavior differed between individuals (χ^2 test, $df = 9$, $\chi^2 = 51.0$, $p < 0.001$). For example, Turtle 5 spent the most time resting (62%) (Fig. S2), whereas Turtle 3 spent most time on 'other behaviors' (74%). The mean water temperature experienced by 9 turtles during their inter-nesting period was $29.5 \pm 0.3^\circ\text{C}$, ranging from 25.8 to 33.3°C . A diel pattern in water temperature was observed, with increases during the day and decreases at night (Fig. S3), for all turtles except IDs 1 and 3, which were tracked during a typhoon that passed over Ishigaki Island.

The proportion of time spent on each behavior changed over the inter-nesting period similarly across individuals, although the proportions differed among individuals (Fig. 5; Fig. S2). The proportion of time spent feeding (including all types) gradually increased from the first day (0.7%) to the middle of the inter-nesting period, reaching 8.7%, but decreased toward the end of the inter-nesting period (0.8%; Fig. 5). In contrast, the proportion of resting decreased toward the middle period (53.5% on the first day to 37.7% on the fifth day), increased for a few days, and decreased again until the end of the period

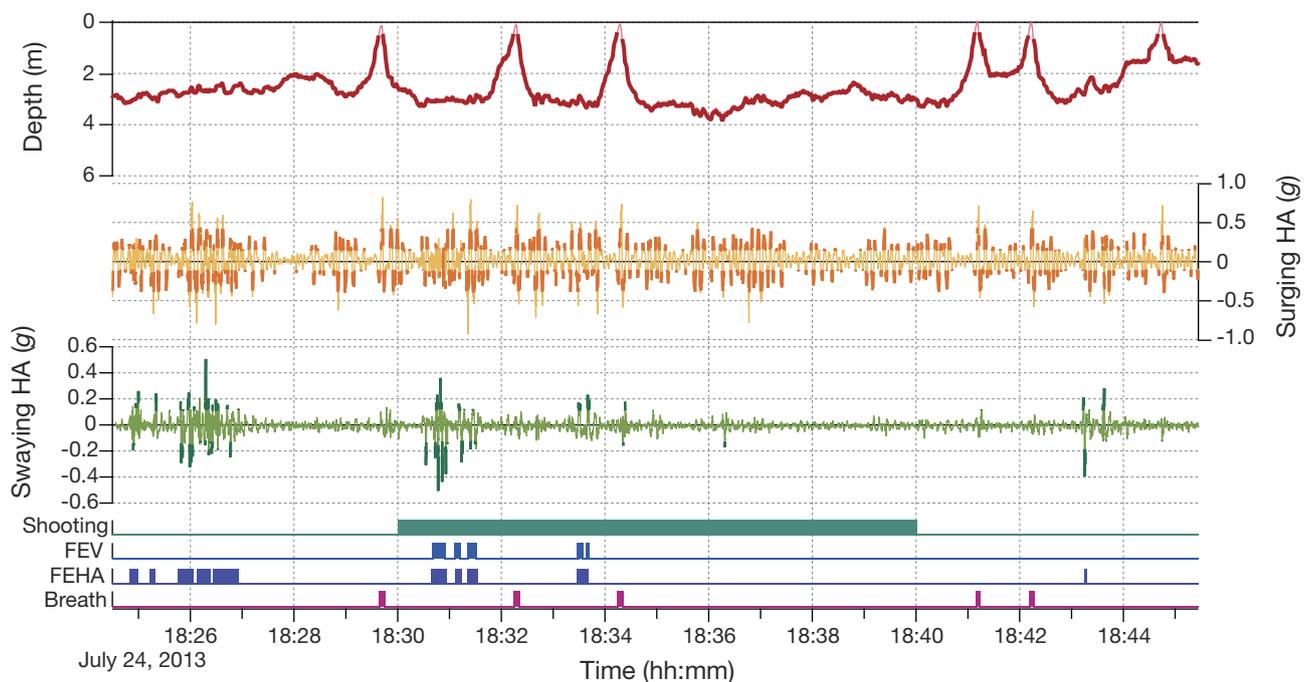


Fig. 3. Typical profiles of depth and the high-frequency components of head acceleration (HA) in the surging and swaying axes in a green turtle (ID 2) during the inter-nesting period. In the profiles, the thin lines with lighter colors represent the high-frequency component data of HA, whereas thick lines with darker colors represent the acceleration data that met the extraction criteria of benthic feeding behavior. The horizontal bars at the bottom indicate the period of video shooting, benthic feeding events observed by the video logger (FEV), feeding events inferred from HA and depth data (FEHA), and breathing events (Breath)

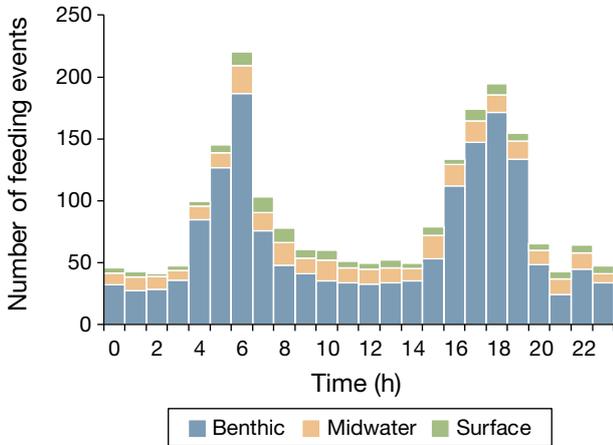


Fig. 4. Diel pattern of the 3 types of feeding events observed during the inter-nesting period in 5 green turtles (IDs 1–5). The head acceleration data recorded for the whole inter-nesting period were used for 4 turtles (IDs 1–3, 5), whereas data recorded for only 3 d were used for Turtle 4 (see Table 1)

(25.7%; Fig. 5). The proportion of ‘other behaviors’ did not show a substantial change from the early to middle period (38.5–50.4%) but then increased toward the end of the inter-nesting period (65.1%; Fig. 5). Individually, ID 3 increased the proportions of time spent midwater feeding and engaged in ‘other behaviors’ during the period (third to fifth day) when the typhoon passed across Ishigaki Island, whereas ID 1 increased the proportion of ‘other behaviors’ during this period (sixth to eighth day; Fig. S2).

3.4. Horizontal movements and home range

Tracking using the Fast-loc GPS logger provided 1082 horizontal location data points from 6 turtles

(IDs 1, 2, and 6–9) during the inter-nesting period. All but one (ID 1) remained in the vicinity of the nesting beach during the inter-nesting period (Fig. 6). The direct distance of the farthest location from each nesting site where the tag had been deployed during the inter-nesting period was 4.1 ± 2.4 km (Fig. S4). Two of the 6 turtles (IDs 2 and 8) remained in shallower waters within the inner reef, whereas 4 remained in deeper waters outside the reef edge (Fig. 6). The home range area during the inter-nesting period varied among individuals; however, all turtles utilized small habitats with 1.1 ± 1.1 and 8.1 ± 9.2 km² of the 50 and 95% FK home ranges, respectively (Fig. 6). However, none of the turtles remained in a single spot during their inter-nesting period, shifting the center of their daily locations by 699 ± 606 m from day to day (Fig. S5). One turtle (ID 1) remained in the southern area of the nesting beach but moved 4.0 km northward to a deeper area when the typhoon passed across Ishigaki Island, following which, she returned to the original area (Fig. 6; Fig. S5).

For 2 turtles (IDs 1 and 2) for which dives, feeding events, and horizontal locations were simultaneously recorded, the location data for feeding (ID 1: N = 91, ID 2: N = 40), resting (ID 1: N = 89, ID 2: N = 84), and ‘other behaviors’ (ID 1: N = 75, ID 2: N = 30) were obtained. Both turtles engaged in benthic feeding in the inner reef around areas where dense seagrass and algal meadows were distributed (Fig. 7). Surface feeding behavior occurred in both the inner and outer reef habitats, whereas midwater feeding was only observed in the outer reef (Fig. 7a,b). ID 1 engaged in bottom resting in relatively deep areas around the outer reef slope, whereas ID 2 engaged in bottom resting in shallow waters within the inner reef (Fig. 7a,b). The core (50% FK isopleths) and usual areas (95%) of the loca-

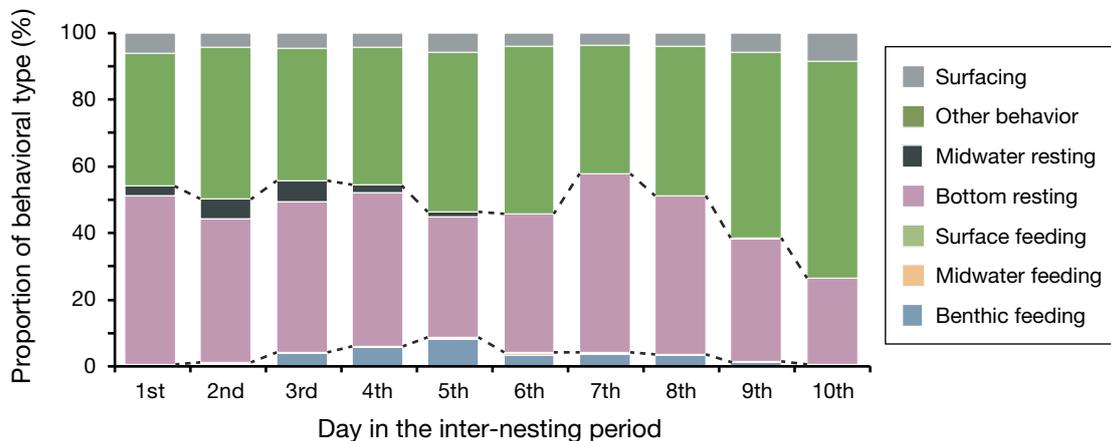


Fig. 5. Time-series of changes in the mean proportions of time spent engaged in each type of behavior during the inter-nesting period in 4 gravid green turtles (IDs 1–3, 5). Dashed lines represent the segmentations between feeding, resting, and ‘other behaviors,’ including surfacing

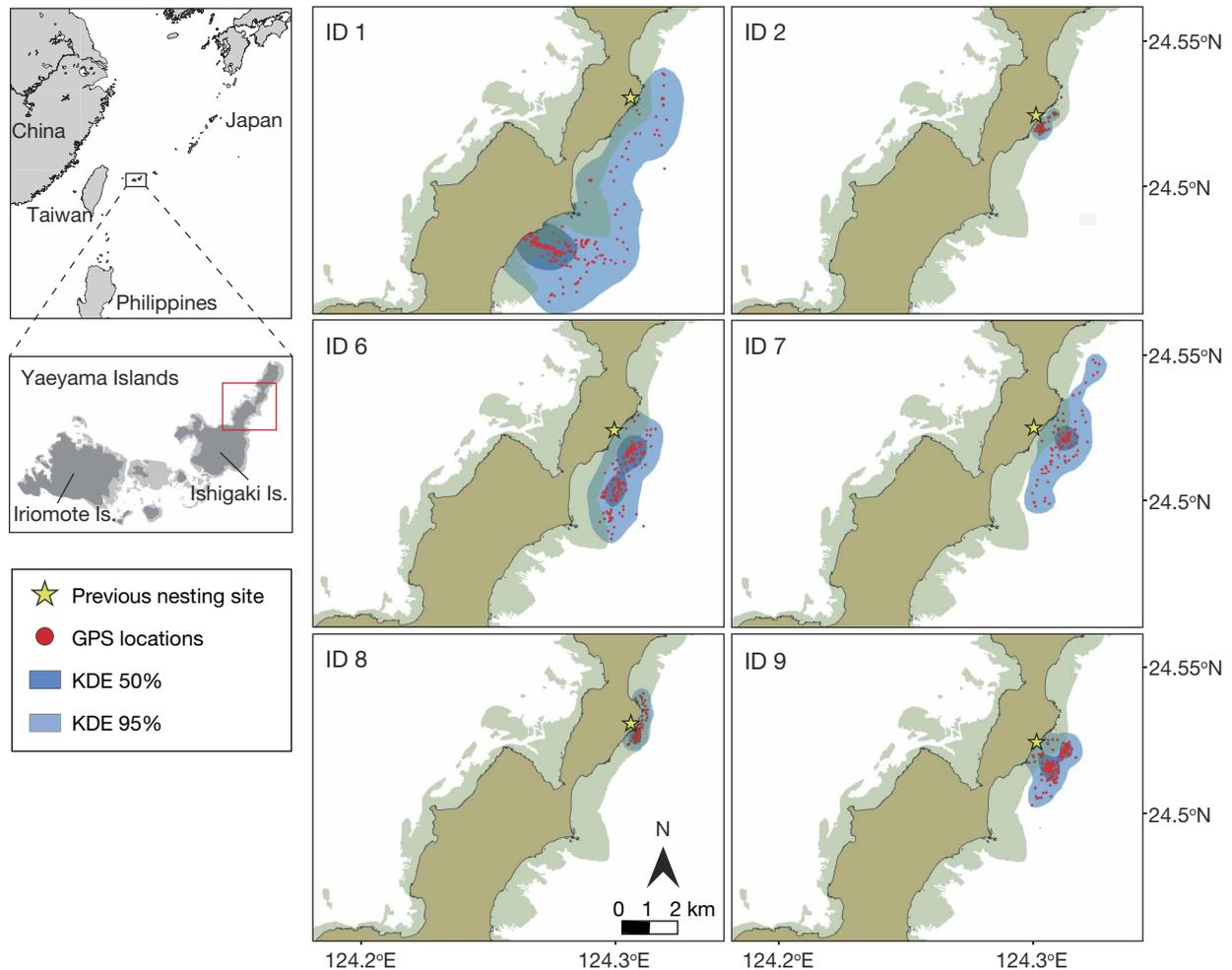


Fig. 6. Locations and the home range of 6 green turtles (IDs 1, 2, 6–9) during the inter-nesting period. The red circles represent the locations of these turtles obtained by the Fast-loc GPS logger. The areas colored by dark and light blue indicate 50 and 95% home ranges, respectively, calculated by the fixed kernel density estimation. Ochre and light green areas indicate the land and fringing reef areas, respectively, of Ishigaki Island. Note that ID 1 was tracked during the period when Typhoon Soulik passed across Ishigaki Island

tions where the turtles engaged in benthic feeding were 0.6 and 5.0 km² for ID 1, whereas the values were 0.5 and 0.8 km² for ID 2, respectively (Fig. 7c,d). Regarding bottom resting, the core and usual areas were 0.4 and 2.1 km² for ID 1, whereas they were 0.1 and 0.4 km² for ID 2, respectively (Fig. 7c,d). The core areas for benthic feeding and bottom resting almost overlapped in both turtles (Fig. 7c,d). The distances between the centers of location data within the core areas for benthic feeding and bottom resting were 289.3 m for ID 1 and 24.8 m for ID 2.

4. DISCUSSION

Our turtles exhibited targeted feeding behavior shuttling between feeding sites and resting places.

These findings suggest that green turtles nesting on Ishigaki Island, where abundant forage is available, feed routinely during inter-nesting periods. However, this 'income breeding' likely makes only a minor contribution to overall breeding effort. Given that green turtles nest approximately once every 4 yr (e.g. Okuyama et al. 2020) and that foraging at feeding grounds occupies approximately 300 d yr⁻¹ (accounting for migrations to and from nesting sites, inclement weather, etc.), these foraging days represent the accumulated resources (capital) used for reproduction, which can be estimated as: 300 d × 4 yr = 1200 d. Assuming an inter-nesting period of 10 d (Table 1) and 6 clutches per breeding period (e.g. Okuyama et al. 2020), the resources gained during the breeding period (income) can be estimated as: 10 d × 5 inter-clutch intervals = 50 d. Consequently, the relative in-

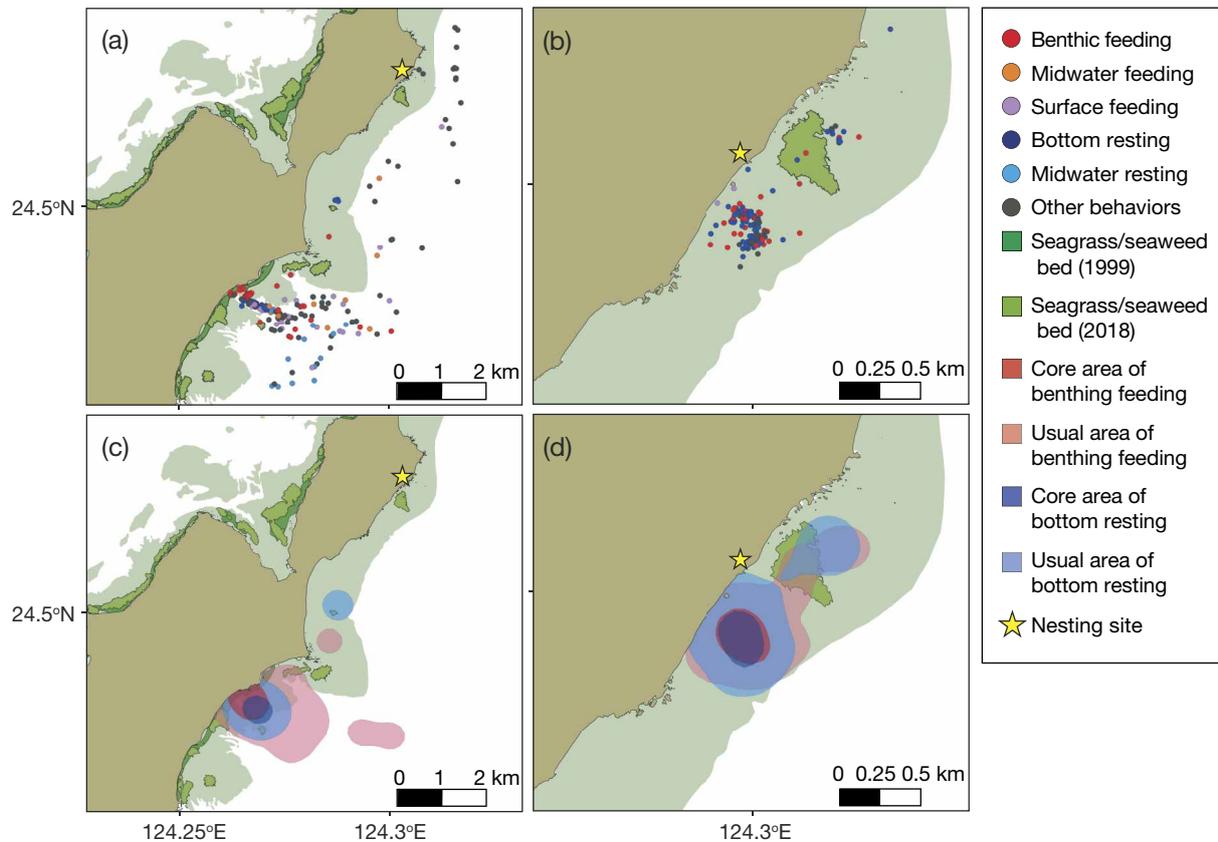


Fig. 7. GPS locations where green turtles (a) ID 1 and (b) ID 2 engaged in feeding, resting, and 'other behaviors.' Core and usual areas, defined as the 50 and 95% utilization distributions, respectively, for benthic feeding and bottom resting, calculated using fixed kernel density estimation, are shown for (c) ID 1 and (d) ID 2. Ochre and light green areas indicate the land and fringing reef areas, respectively, of Ishigaki Island

come component is calculated as: $100\% \times 50 \text{ d} / (50 \text{ d} + 1200 \text{ d}) = 4.0\%$. The actual income contribution may be even lower than this estimate, given that the gut content during the inter-nesting period is known to be lower than during the foraging period (Stokes et al. 2019). Indeed, immature turtles inhabiting Iriomote Island — adjacent to Ishigaki Island — were observed to spend an average of 4.8 h d^{-1} feeding (Okuyama et al. 2013), whereas gravid turtles in our study exhibited a maximum daily feeding duration of only 2.1 h (8.7%). However, the method used by Okuyama et al. (2013) may slightly overestimate feeding time compared to our approach in the present study. Furthermore, several studies from other regions have reported feeding durations for non-gravid green turtles ranging from 5 to 12 h d^{-1} (Bjorndal 1980, Mendonça 1983, Williams 1988, Taquet et al. 2006, MacDonald et al. 2013). Although this estimation is based on hypothetical calculations and several assumptions, it suggests that the energy income acquired during the inter-nesting period is unlikely to be substantial, probably sufficient only to meet daily metabolic

requirements rather than significantly contributing to the energy demands of egg production. Moreover, the proportion of time spent resting was almost half of the inter-nesting period (42.1% on average), indicating that energy-saving behavior through resting is a substantial behavioral strategy for green turtles during the inter-nesting period. Therefore, we conclude that they employ a mixed capital–income breeding strategy wherein females mostly rely on capital reserves, with a small input from income, as reported in fish (cf. McBride et al. 2015).

Most of the benthic feeding behavior occurred around dense seagrass and seaweed meadows and near the sites where bottom/midwater resting behavior was observed, indicating that turtles use very little energy shuttling between feeding and resting sites. The slight differences in location between benthic feeding and dense seagrass/seaweed beds may indicate that the turtles foraged in areas where seagrass and seaweed were present, but patchy, rather than abundant. Alternatively, it is also possible that the area with dense seagrass/seaweed changed between

2013, when the turtles were tracked, and 1999/2018, when the distribution data of seagrass/seaweed were obtained. The sites where benthic feeding behavior occurred were concentrated within small core areas near the seagrass/seaweed bed, indicating that green turtles repeatedly utilized the same benthic feeding habitat during the inter-nesting period. Such continuous use of foraging sites is common in green turtles during non-breeding periods (Okuyama et al. 2013, Shimada et al. 2020, Siegwalt et al. 2020).

Green turtles nesting on Ishigaki Island showed a clear diel rhythm of benthic feeding, with 2 peaks per day at approximately 06:00 and 18:00 h during the inter-nesting period. These periods correspond to the times just after sunrise and just before sunset, encompassing the crepuscular periods on Ishigaki Island. Notably, this pattern is similar to that observed for immature green turtles inhabiting the Yaeyama Islands, including Ishigaki Island (Okuyama et al. 2013, J. Okuyama unpubl. data). The reason why gravid and immature green turtles exhibit similar feeding patterns is unclear. In agreement with the results reported by Okuyama et al. (2013), there was no relationship between the number of benthic feeding events and the tidal levels in this study (Fig. S6). Okuyama et al. (2013) suggested that the bimodal feeding pattern in immature turtles was due to the time needed to digest the seagrass ingested in the morning, resulting in 2 peaks. However, larger turtles may be able to continuously feed on seagrass throughout the daytime because of their larger gut capacity and faster processing rate (Bjørndal 1980); our results did not support this hypothesis (Okuyama et al. 2013). Water temperature also affects the digestive efficiency of green turtles (Bjørndal 1980). However, the water temperatures reported by Okuyama et al. (2013) and those in our study are very similar, with mean temperatures ranging between 28 and 30°C. Stokes et al. (2019) reported that gravid turtles have less gut content than adult males and non-breeding females, likely because energy conservation for egg clutch maturation takes priority over foraging, and the developing eggs occupy significant internal space, limiting gut capacity. These factors may reduce feeding duration and gut capacity in gravid turtles, resulting in a similar feeding pattern to that observed in immature turtles (Okuyama et al. 2013). Alternatively, the turtles may rest in warmer waters during the day to facilitate egg maturation (Fig. S3).

Midwater feeding is a common feeding pattern in sea turtles (Wallace et al. 2015, Okuyama et al. 2021, Fujita et al. 2023). The gravid green turtles in our study also fed on drifting and floating algae and sea-

grass. Midwater feeding occurred only in relatively deep waters outside the reef edge, whereas surface feeding occurred in both the inner and outer reefs. The food items of both midwater and surface feeding were mainly drifting/floating seagrass, and the time spent on these feeding types increased during the period when a typhoon passed over the area where 2 turtles (IDs 1 and 3) were located. This increase was presumably because there was plentiful drifting/floating seagrass and algae sloughed off from the substrates by strong currents and swells, and the turtles had many chances to encounter this drifting food. Such encounters with drifting/floating food items generally seemed to be rare in the restricted inter-nesting habitat. Therefore, feeding on drifting/floating appears to be opportunistic rather than targeted.

The main food items consumed by our turtles were algae and seagrass. Animal matter was rarely recorded, although green turtles nesting on Raine Island, Australia, have been observed to consume animal matter (Tucker & Read 2001). Moreover, our video data did not support the hypothesis that gravid sea turtles feed on calcareous materials for eggshell formation (Tucker & Read 2001, Stokes et al. 2019), although there were some limitations in identifying food species based on our video footage.

Green turtles nesting on Ishigaki Island established their core area (50% FK home range) in the inner reef and just outside the reef edges, near their nesting sites. Similar patterns of restricted offshore movements during the inter-nesting period have been reported previously in green turtles (Liew & Chan 1992, Taquet et al. 2006, Blanco et al. 2013, Chambault et al. 2016, Esteban et al. 2017, Raposo et al. 2023).

In this study, we observed a shift in time allocated to feeding and resting by turtles throughout the inter-nesting period. While previous research has not examined time-series changes in the feeding behavior during this period, studies have documented temporal variations in dive patterns. These studies have shown that turtles decrease and increase the proportion of resting and active dives, respectively, at the beginning, end, or both of the inter-nesting period (Hochscheid et al. 1999, Houghton et al. 2002, Cheng 2009). Fossette et al. (2012) reported that gravid turtles increased their activity levels in cold water, which they attributed to thermoregulation. However, the water temperature during our study (averaging 29.5°C, see Fig. S3) was within a range considered sufficiently warm to preclude such behavior. Furthermore, no extended periods at the surface indicative of basking were observed in either the video or the depth data. In

contrast to previous studies, the turtles in our study spent more time feeding instead of resting during the middle of the inter-nesting period (feeding: 8.6% vs. resting: 37.7% on the fifth day, compared to 0.7 vs. 53.5% on the first day of the inter-nesting period). These observations highlight a distinct behavioral pattern in green turtles nesting on Ishigaki Island: they moved to their core area on the first day after nesting and subsequently increased feeding time while resting within this core area. As the next nesting event approached, feeding time decreased, and active swimming time increased, with the turtles moving closer to the nesting beach (Fig. 5; Fig. S4). These behavioral changes may represent preparation for the subsequent nesting event.

The 2 turtles tracked when the typhoon passed across Ishigaki Island (IDs 1 and 3) increased the proportion of time spent on 'other behaviors' (Fig. S2), consistent with previous reports of increased activity or deeper diving behavior in turtles encountering hurricanes/typhoons (Sakamoto et al. 1990, Storch et al. 2006, Wilson et al. 2017). This increased activity, potentially including movements to deeper outer reefs, may have contributed to the wider home range observed for turtle ID 1.

Of the 7 sea turtle species, only green turtles have been reported to feed frequently during the inter-nesting period at nesting sites where food is abundant (Balazs 1980, Tucker & Read 2001, Hays et al. 2002b, Fuller et al. 2009, Stokes et al. 2019, this study). Why are green turtles the only sea turtles reported to feed during the inter-nesting period? We suggest that, at least in our study, the abundance of benthic food sources close to the nesting beach is the most likely explanation. In such circumstances, there are almost no traveling costs for shuttling between feeding sites, resting places, and the nesting beach. In other sea turtle species, food sources may not be located near the nesting beach, so it is not energetically advantageous to shuttle between the nesting beach and food sources during the inter-nesting period. We conclude that nesting green turtles generally employ an energy-saving strategy with frequent resting dives for subsequent nesting events during the inter-nesting period, as has been reported for other sea turtles (Hays et al. 2000, Hamann et al. 2002). However, when abundant food is available adjacent to the nesting beach, green turtles target these areas to supplement their energy budget during nesting. Further studies are needed to further quantify the importance of energy gained from foraging during the inter-nesting period to the overall energetics of breeding.

Acknowledgements. This study was partially supported by the Environment Research and Technology Development Fund (JPMEERF20244003) of the Environmental Restoration and Conservation Agency provided by the Ministry of the Environment of Japan, and by a Grant-in-Aid for JSPS Young Scientists B (JO No. 22710236). We acknowledge H. Kamihata, T. Hashiguchi, H. Watanabe, A. Nakabayashi, and Y. Kami from Kyoto University, D. Imakita and K. Watajima from Kindai University, and S. Tanizaki and H. Ishii from the Ishigaki Island Sea Turtle Research Group for their assistance. This study was conducted with permission from the Fisheries Adjustment Commission of Okinawa Prefecture (4-2, 21-23, 25-1) and the Ministry of the Environment, Japan (090721001, 10063001, 2207282). The research protocol, including the deployment of the bio-logging devices, was approved by the Animal Experimentation Committee of Kyoto University (Inf-K25-4).

LITERATURE CITED

- Balazs GH (1980) Synopsis of the biological data on the green turtle in the Hawaiian Islands. Tech Memo NOAA-TM-NMFS-SWFC-7
- ✦ Ballorain K, Bourjea J, Ciccione S, Kato A and others (2013) Seasonal diving behaviour and feeding rhythms of green turtles at Mayotte Island. *Mar Ecol Prog Ser* 483:289–302
- Biodiversity Center of Japan, Ministry of the Environment (2021) Report of Fourth National Basic Survey on Natural Environment. <http://gis.biodic.go.jp/webgis/index.html> (accessed on 5 December 2023) (in Japanese)
- ✦ Bjorndal KA (1980) Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Mar Biol* 56:147–154
- ✦ Blanco GS, Morreale SJ, Seminoff JA, Paladino FV, Piedra R, Spotila JR (2013) Movements and diving behavior of inter-nesting green turtles along Pacific Costa Rica. *Integr Zool* 8:293–306
- ✦ Bonnet X, Bradshaw D, Shine R (1998) Capital versus income breeding: an ectothermic perspective. *Oikos* 83:333–342
- Calenge C (2011) Home range estimation in R: the adehabitat-HR package (v. 0.4.22.). <https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf>
- ✦ Carr A, Ross P, Carr S (1974) Internesting behavior of the green turtle, *Chelonia mydas*, at a mid-ocean island breeding ground. *Copeia* 1974:703–706
- ✦ Casey J, Garner J, Garner S, Williard AS (2010) Diel foraging behavior of gravid leatherback sea turtles in deep waters of the Caribbean Sea. *J Exp Biol* 213:3961–3971
- Chambault P, de Thoisy B, Kelle L, Berzins R and others (2016) Inter-nesting behavioural adjustments of green turtles to an estuarine habitat in French Guiana. *Mar Ecol Prog Ser* 555:235–248
- ✦ Cheng I (2009) Changes in diving behaviour during the inter-nesting period by green turtles. *J Exp Mar Biol Ecol* 381:18–24
- Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252
- ✦ Dujon AM, Lindstrom RT, Hays GC (2014) The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods Ecol Evol* 5:1162–1169
- ✦ Esteban N, Mortimer JA, Hays GC (2017) How numbers of nesting sea turtles can be overestimated by nearly a factor of two. *Proc R Soc B* 284:20162581
- ✦ Fossette S, Gaspar P, Handrich Y, Le Maho Y, Georges JY (2008) Fine-scale diving behaviour and beak movements

- in leatherback turtles (*Derموchelys coriacea*) nesting in French Guiana. *J Anim Ecol* 77:236–246
- ✦ Fossette S, Schofield G, Lilley MK, Gleiss AC, Hays GC (2012) Acceleration data reveal the energy management strategy of a marine ectotherm during reproduction. *Funct Ecol* 26:324–333
- ✦ Freitas C, Caldeira R, Reis J, Dellinger T (2018) Foraging behavior of juvenile loggerhead sea turtles in the open ocean: from Lévy exploration to area-restricted search. *Mar Ecol Prog Ser* 595:203–215
- ✦ Fujita K, Nishizawa H, Okuyama J, Arita M, Takuma S, Narazaki T, Watabe A (2023) Polymorphic foraging tactics in a marine reptile: insight from horizontal movement and dive behavior analyses. *Mar Ecol Prog Ser* 707:115–129
- ✦ Fuller WJ, Broderick AC, Hooker SK, Witt MJ, Godley BJ (2009) Insights into habitat utilization by green turtles (*Chelonia mydas*) during the inter-nesting period using animal-borne digital cameras. *Mar Technol Soc J* 43: 51–59
- ✦ Hamann M, Limpus CJ, Whittier JM (2002) Patterns of lipid storage and mobilisation in the female green sea turtle (*Chelonia mydas*). *J Comp Physiol B* 172:485–493
- Hamann M, Limpus CJ, Owens DW (2003) Reproductive cycles of males and females. In: Lutz PL, Musick JA, Wyneken J (eds) *The biology of sea turtles*, Vol 2. CRC Press, Boca Raton, FL, p 135–161
- ✦ Hays GC, Adams CR, Broderick AC, Godley BJ, Lucas DJ, Metcalfe JD, Prior AA (2000) The diving behavior of green turtles at Ascension Island. *Anim Behav* 59:577–586
- ✦ Hays GC, Broderick AC, Glen F, Godley BJ (2002a) Change in body mass associated with long-term fasting in a marine reptile: the case of green turtles (*Chelonia mydas*) at Ascension Island. *Can J Zool* 80:1299–1302
- ✦ Hays GC, Glen F, Broderick AC, Godley BJ, Metcalfe JD (2002b) Behavioral plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. *Mar Biol* 141: 985–990
- ✦ Hochscheid S, Godley BJ, Broderick AC, Wilson RP (1999) Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Mar Ecol Prog Ser* 185: 101–112
- ✦ Houghton JDR, Broderick AC, Godley BJ, Metcalfe JD, Hays GC (2002) Diving behaviour during the interesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Mar Ecol Prog Ser* 227:63–70
- ✦ James MC, Ottensmeyer CA, Eckert SA, Myers RA (2006) Changes in diel diving patterns accompany shifts between northern foraging and southward migration in leatherback turtles. *Can J Zool* 84:754–765
- ✦ Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78: 57–66
- Liew HC, Chan EH (1992) Biotelemetry of green turtles (*Chelonia mydas*) in Pulau Redang, Malaysia during the interesting period. In: Mancini P, Fioretti S, Cristalli C, Bedini R (eds) *Proc 12th Biotelemetry Conf*. Editric Universitaria Litografia Felia, Ancona, p 157–163
- ✦ MacDonald BD, Lewison RL, Madrak SV, Seminoff JA, Eguichi T (2013) Seasonal and diel variability in site visitation and movement behavior of East Pacific green turtles, *Chelonia mydas*, in a highly urbanized temperate foraging ground. *J Exp Mar Biol Ecol* 443:56–64
- ✦ McBride RS, Somarakis S, Fitzhugh GR, Albert A and others (2015) Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish Fish* 16:23–57
- ✦ Mendonça MT (1983) Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. *Copeia* 1983:1013–1023
- Miller JD (1997) Reproduction in sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*. CRC Press, Boca Raton, FL, p 51–82
- ✦ Minamikawa S, Naito Y, Uchida I (1997) Buoyancy control in diving behavior of the loggerhead turtle, *Caretta caretta*. *J Ethol* 15:109–118
- ✦ Mortimer JA, Portier KM (1989) Reproductive homing and interesting behavior of the green turtle (*Chelonia mydas*) at Ascension Island, South Atlantic Ocean. *Copeia* 1989:962–977
- ✦ Okuyama J, Kawabata Y, Naito Y, Arai N, Kobayashi M (2009) Monitoring beak movements with an acceleration datalogger: a useful technique for assessing the feeding and breathing behaviors of sea turtles. *Endang Species Res* 10:39–45
- ✦ Okuyama J, Shimizu T, Abe O, Yoseda K, Arai N (2010) Wild versus head-started hawksbill turtles *Eretmochelys imbricata*: post-release behavior and feeding adaptations. *Endang Species Res* 10:181–190
- ✦ Okuyama J, Nakajima K, Noda T, Kimura S and others (2013) Ethogram of immature green turtles: behavioral strategies for somatic growth in large marine herbivores. *PLOS ONE* 8:e65783
- ✦ Okuyama J, Seminoff JA, Dutton PH, Benson SR (2016) Fine-scale monitoring of routine deep dives by gravid leatherback turtles during the inter-nesting interval indicate a capital breeding strategy. *Front Mar Sci* 3:166
- ✦ Okuyama J, Ishii H, Tanizaki S, Suzuki T and others (2020) Quarter-century (1993–2018) nesting trends in the peripheral populations of three sea turtle species at Ishigakijima Island, Japan. *Chelonian Conserv Biol* 19:101–110
- ✦ Okuyama J, Benson SR, Dutton PH, Seminoff JA (2021) Changes in dive patterns of leatherback turtles with sea surface temperature and potential foraging habitats. *Ecosphere* 12:e03365
- ✦ Plot V, Jenkins T, Robin JP, Fossette S, Georges JY (2013) Leatherback turtles are capital breeders: morphometric and physiological evidence from longitudinal monitoring. *Physiol Biochem Zool* 86:385–397
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Raposo C, Mestre J, Rebelo R, Regalla A, Davies A, Barbosa C, Patrício AR (2023) Spatial distribution of inter-nesting green turtles from the largest Eastern Atlantic rookery and overlap with a marine protected area. *Mar Ecol Prog Ser* 703:161–175
- ✦ Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLOS ONE* 4:e5379
- ✦ Sakamoto W, Uchida I, Naito Y, Kureha K, Tujimura M, Sato K (1990) Deep diving behavior of the loggerhead turtle near the frontal zone. *Bull Jpn Soc Sci Fish* 56:1435–1443
- ✦ Santos AJB, Freire EMX, Bellini C, Corso G (2010) Body mass and the energy budget of gravid hawksbill turtles (*Eretmochelys imbricata*) during the nesting season. *Herpetologica* 44:352–359

- ✦ Schofield G, Katselidis KA, Dimopoulos P, Pantis JD, Hays GC (2006) Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. *Endang Species Res* 2:71–79
- ✦ Shimada T, Limpus CJ, Hamann M, Bell I, Esteban N, Groom R, Hays GC (2020) Fidelity to foraging sites after long migrations. *J Anim Ecol* 89:1008–1016
- ✦ Shine R (2003) Reproductive strategies in snakes. *Proc R Soc B* 270:995–1004
- ✦ Siegwalt F, Benhamou S, Girondot M, Jeantet L and others (2020) High fidelity of sea turtles to their foraging grounds revealed by satellite tracking and capture-mark-recapture: new insights for the establishment of key marine conservation areas. *Biol Conserv* 250:108742
- ✦ Southwood AL, Andrews R, Paladino FV, Jones DR (2005) Effects of diving and swimming behavior on body temperatures of Pacific leatherback turtles in tropical seas. *Physiol Biochem Zool* 78:285–297
- Stearns SC (1992) *The evolution of life histories: theory and analysis*. Oxford University Press, Oxford
- ✦ Stokes HJ, Mortimer JA, Hays GC, Unsworth RK, Laloë JO, Esteban N (2019) Green turtle diet is dominated by seagrass in the Western Indian Ocean except amongst gravid females. *Mar Biol* 166:135
- ✦ Storch S, Hays GC, Hillis-Starr Z, Wilson DP (2006) The behaviour of a hawksbill turtle data-logged during the passage of hurricane Georges through the Caribbean. *Mar Freshw Behav Physiol* 39:307–313
- Swimmer Y, Arauz R, Higgins B, McNaughton L, McCracken M, Ballesterio J, Brill R (2005) Food color and marine turtle feeding behavior: Can blue bait reduce turtle bycatch in commercial fisheries? *Mar Ecol Prog Ser* 295:273–278
- ✦ Tanaka H, Sato K, Matsuzawa Y, Sakamoto W, Naito Y, Kuroyanagi K (1995) Analysis of possibility of feeding of loggerhead turtles during interesting periods based on stomach temperature measurements. *Bull Jpn Soc Sci Fish* 61:339–345 (in Japanese with English abstract)
- ✦ Taquet C, Taquet M, Dempster T, Soria M, Ciccione S, Roos D, Dagorn L (2006) Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. *Mar Ecol Prog Ser* 306:295–302
- ✦ Tucker AD, Read MA (2001) Frequency of foraging by gravid green turtles (*Chelonia mydas*) at Raine Island, Great Barrier Reef. *J Herpetol* 35:500–503
- ✦ van Dam RP, Diez CE (1997) Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. *Coral Reefs* 16:133–138
- ✦ Wallace BP, Zolkewitz M, James MC (2015) Fine-scale foraging ecology of leatherback turtles. *Front Ecol Evol* 3:15
- ✦ Williams SL (1988) *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. *Mar Biol* 98:447–455
- ✦ Wilson M, Tucker AD, Beedholm K, Mann DA (2017) Changes of loggerhead turtle (*Caretta caretta*) dive behavior associated with tropical storm passage during the inter-nesting period. *J Exp Biol* 220:3432–3441
- ✦ Yasuda T, Arai N (2009) Changes in flipper beat frequency, body angle and swimming speed of female green turtles *Chelonia mydas*. *Mar Ecol Prog Ser* 386:275–286

Editorial responsibility: Graeme Hays, Burwood, Victoria, Australia

Reviewed by: S. Fossette and D. Booth, and previous version reviewed in MEPS by Y. Kaska and 2 anonymous referees

Submitted: April 18, 2025; Accepted: April 23, 2025

Proofs received from author(s): July 3, 2025

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