Anatomical evidence that arribada olive ridley sea turtles *Lepidochelys olivacea* feed at breeding and nesting grounds to maintain high reproductive output

Brianna L. Myre[1,5,*], **Christine Figgener**[2], **Brendon Byrd**[1,6], **A. Nicole Guentzel**[1], **Pamela T. Plotkin**[2,3,4], **Joseph Bernardo**[1,2], **Duncan S. MacKenzie**[1,2]

[1]Department of Biology, Texas A&M University, College Station, TX 77843, USA
[2]Marine Biology Interdisciplinary Program, Texas A&M University, College Station, TX 77843, USA
[3]Department of Oceanography, Texas A&M University, College Station, TX 77843, USA
[4]Texas Sea Grant, College Station, TX 77843, USA

[5]*Present address:* Department of Biology, Hastings College, Hastings, NE 68901, USA

[6]*Present address*: School of Biological Sciences, University of Oklahoma, Norman, OK 73019, USA

ABSTRACT: Several sea turtle life histories display a capital breeding pattern, in which females stockpile resources, like fat, during reproductive quiescence to fuel fasted egg production. The olive ridley *Lepidochelys olivacea* nests annually, restricting resource accumulation time, which may necessitate an income-like strategy. To evaluate the breeding strategy of olive ridleys nesting in Ostional, Costa Rica, 123 females were examined during mating or nesting from mid-June to early September in 2016 and 2017. We recaptured 9 females once and 2 females twice 2—6 wk apart, and 112 other females were sorted by behavior (mating/nesting) and ovarian state (non-atretic/atretic) to determine if body condition score (BCS) or subcutaneous fat layer thickness (SQFT) declined over the season, as expected in capital breeders. We calculated BCS and measured SQFT with ultrasound to quantify stored resources, and egg number, egg mass and ovarian follicle size for reproductive output. Two different BCS calculations did not correlate with SQFT. The 2016 female SQFTs showed a capital breeding pattern, with a significantly thicker initial SQFT, and a decline when recaptured that season; 2017 showed a more income-like pattern, with thinner initial SQFTs and no change at recapture. Intestinal contents (suggesting feeding) were found more frequently in 2017, while reproductive output showed no differences. The differences in SQFT and intestinal content frequency between years suggest olive ridleys may use an intermediate breeding strategy to facilitate resilience in fecundity when facing environmental fluctuations.

KEY WORDS: Breeding strategies · Capital breeding · Income breeding · Ultrasound · *Lepidochelys olivacea* · El Niño Southern Oscillation · Body condition · Sea turtle

1. INTRODUCTION

The physiological challenge of sea turtle reproduction lies in its high output, as sea turtles lay more eggs than any other reptile. Sea turtles couple high reproductive output with long migrations from feeding grounds to distant nesting beaches, meaning a multi-year breeding cycle for resource recovery must provide the foundation for the classic capital breeding pattern, where energetic requirements for reproduction are met by using stored resources obtained prior to reproductive migration. In contrast, income breeders continue concurrent energy intake over the reproductive period. For green *Chelonia mydas* (Hamann et al. 2002), leatherback *Dermochelys coriacea* (Plot et al. 2013, Perrault et al. 2014), loggerhead *Caretta*

*Corresponding author: brie.myre@hastings.edu

caretta (Perrault & Stacy 2018), and hawksbill *Eretmochelys imbricata* (Santos et al. 2010, Goldberg et al. 2013) sea turtles, a variety of stable isotope, body morphometric and physiological evidence supports their classification as capital breeders. However, this pattern may not be present in ridley sea turtles *Lepidochelys* spp., which nest annually (Valverde et al. 2012) and so do not have extended periods for resource stockpiling prior to the next reproductive season.

Lepidochelys is the only sea turtle genus with mass-nesting events (termed 'arribadas') where hundreds to thousands of females emerge synchronously over periods of several days to deposit their clutches. The olive ridley sea turtle *L. olivacea* is a highly nomadic, pelagic species that lacks discrete migratory corridors and commonly revisited foraging grounds (Plotkin 1994, 2010, Plotkin & Bernardo 2003). These unique aspects of its behavior could mean that an income strategy may be more advantageous for this species. The Eastern Tropical Pacific (ETP) population nests near an area of extremely high nutritive resource availability due, in part, to the upwelling which occurs in the area, bringing nutrition-dense cold water to the surface, as well as its proximity to the Costa Rican Thermal Dome, a primary productivity hotspot (Jimenez 2017). These features suggest feeding could continue in these nutrient dense waters. ETP olive ridleys are thus an ideal population to evaluate metrics for measuring capital and income breeding. If olive ridleys are income breeders, potential prey species should be monitored and managed near nesting beaches to ensure maximal reproductive output. In this study, we have therefore applied several approaches to assess nutrient utilization during the nesting period in a Costa Rican population of olive ridleys to determine whether there is evidence that they use an income breeding strategy.

Olive ridleys are the most abundant sea turtle species in the world (Cáceres-Farias et al. 2022). Adults forage across a massive 3200 km neritic habitat from Mexico to Peru, and most migrate to breeding areas in late June, then concentrate near nesting beaches about 30–45 d prior to first nesting for mating (Plotkin 1994). Part of the female population will emerge 2–6 wk later in high numbers to nest synchronously in an arribada over several days (Valverde et al. 2012), laying about 100 eggs per clutch (Jensen et al. 2006). At Ostional, the largest arribada nesting beach in Costa Rica, arribadas occur about 1 mo apart. Arribadas are comprised of both first-nesting females and females who have nested in a previous arribada (Plotkin et al. 1997). Females ovulate their next clutch about 48 h post-nesting (Licht et al. 1982). The clutch will be fully shelled and ready to be laid in the next 14 d, although arribada turtles have been known to hold eggs in the distal oviduct until an unknown cue signals the onset of the next arribada (Plotkin et al. 1997, Williamson et al. 2019). A female typically lays 1–3 clutches per season before departing to return to foraging areas (Plotkin 1995), and most males depart by mid-September (Plotkin et al. 1996).

Determining whether olive ridleys nesting at Ostional are income breeders is challenging because directly observing feeding behavior is difficult in nomadic marine animals. The body condition score (BCS), a well-established metric for assessing nutrient storage and health of sea turtles, could provide evidence for an income strategy if the BCS is maintained from early to late season, indicating significant fat is not being mobilized. BCSs are often calculated as modified weight—length relationships and are intended to be used as a metric of 'fatness' or 'well-being' (Tesch 1971). Fulton's condition factor (FCF), a mass—length relationship derived from Galileo's cube law (Mazzotti et al. 2012), has been commonly used in diverse species, including sea turtles (Bjorndal 1985, Seminoff et al. 2004, Keller et al. 2005, Clukey et al. 2017, Lamont & Johnson 2021). Alternatively, relative body condition, K_{rel}, was developed for sea turtles as a more sensitive index of health (Labrada-Martagon et al. 2014). Previously, BCSs have been useful in sea turtles for detecting mass loss associated with a reduction of foraging and mobilization of energy stores due to boat strike injury, habitat pollution (Labrada-Martagon et al. 2014), fibropapillomatosis prevalence (Rossi et al. 2019), and human interaction (Stewart et al. 2016). However, the utility of these scores has been questioned (Jakob et al. 1996, Schulte-Hostedde et al. 2001, Labrada-Martagon et al. 2014).

We propose that evaluating resource storage with ultrasound examination may provide a more sensitive and precise measure of nutrient intake and utilization. We test this in sea turtles by comparing 2 different BCSs to ultrasound measurements of subcutaneous fat layer thickness (SQFT), a technique developed in leatherback turtles (Harris et al. 2016). We hypothesized that if olive ridleys are capital breeders, SQFT should decline over time from arrival at the nesting beach through each subsequent nesting event. Likewise, ultrasound examination is used to estimate the reproductive stage of amphibian, non-avian reptile, and bird species, including sea turtles (Rostal et al. 1990, Casares et al. 1997, Hofbauer & Krautwald-Junghanns 1999, Myre et al. 2016, Dikikh et al. 2024). We used this method to stage each female by revealing the presence of vitellogenic follicles,

shelled oviductal eggs, and/or atretic follicles. The presence of atretic follicles has been used previously to distinguish between early and late nesting season sea turtles (Rostal et al. 1990, Valente et al. 2011, Myre et al. 2016). Atretic follicle presence in females that were confirmed to be post-intromission indicates the female is likely preparing a final clutch and resorbing follicle contents in preparation for the return migration back to feeding grounds (Rostal et al. 1990). Atretic follicles can also be seen early in or during the nesting season due to poor health or inadequate nutrition (Manire et al. 2017). For these reasons, comparing atretic to non-atretic females is a useful contrast to include when assessing tools for determining nutritional status. Additionally, because olive ridleys are omnivorous, we expect them to consume a variety of prey containing connective tissues such as skeletons or exoskeletons that appear hyperechoic and so are expected to be visible during inguinal ultrasound through the distal intestines (Pease et al. 2010), indicating recent food consumption from within the last 1−5 wk estimated from gut transit studies in other sea turtle species (Burke et al. 1994, Di Bello et al. 2006, Amorocho & Reina 2008, Valente et al. 2008). Together, these metrics should help elucidate if and how olive ridleys might primarily utilize stored nutrients to fuel the energy requirements of multiple nesting, and whether inter-annual climatic fluctuations impact energy utilization for reproduction.

Periods of interannual warming result in large-scale changes to the food web that olive ridleys rely on to stockpile nutritive resources between breeding seasons. One such event is the anomalous marine heatwave of 2016. This event resulted in elevated sea surface temperatures (SST), reduced upwelling, and nutrient poor water. Similar events reduced food availability for higher trophic levels, resulting in reduced growth rates in sea turtles and birds (Bjorndal et al. 2003, Saba et al. 2007, Ancona et al. 2011) and low reproductive output in sea turtles and birds (Ancona & Drummond 2013, Arendt et al. 2013, Saragoça Bruno et al. 2020). The 2016 heat wave was strong enough to reduce sightings of endangered humpback whales *Megaptera novaengliae* in the Costa Rican southern Pacific, potentially reducing the number of calving females returning to southern Costa Rica that season (Pelayo-González et al. 2022). ETP humpback whales also may share feeding grounds off the western coast of North America with olive ridleys, and so both species may have experienced similar resource reduction due to the anomalous heat wave. In concert with this wave, El Niño Southern Oscillation (ENSO) also causes increased SST, and as a result, ocean productivity declines (Timmermann et al. 1999), further reducing food availability. The strongest ENSO event in 18 yr occurred in 2016, and the documented increase in SST occurred over 18 mo (September 2014−May 2016). This ENSO dramatically affected tropical forest biomass that did not recover by 2017 (Wigneron et al. 2020). We aimed to sample across years to assess whether inter-annual variation in climate affected olive ridley reproductive strategy. Changing breeding strategy according to environmental conditions has been documented in reptiles, such as the aquatic snake *Seminatrix pygaea* (Winne et al. 2006). This flexibility of breeding strategy was credited for allowing this species to maintain its reproductive output following years of low resource acquisition. To evaluate the nutritive state in olive ridleys, we collected data on physiological and morphometric characteristics of females exhibiting specific behaviors (mating or arribada nesting) indicative of reproductive condition from courtship to late nesting (when females are preparing to return to feeding areas), to identify capital-like or income-like patterns. In this study, we have therefore applied several approaches to assess nutrient utilization during the nesting period in a Costa Rican population of olive ridleys to determine whether there is evidence that they use an income breeding strategy.

2. MATERIALS AND METHODS

2.1. Sampling site

All sampling was covered under The National Commission for the Management of Biodiversity (CONAGEBIO) permit, R-029-2016-OT-CONAGEBIO, and the National System of Conservation Areas and Costa Rican Ministry of the Environment (SINAC/MINAE) permit no. ACG-PI-026-2016, as well as TAMU IACUC approval 2016-0169. We examined wild olive ridley turtles in Ostional, Guanacaste, Costa Rica, from mid-June to early September 2016 (n = 60) and 2017 (n = 65). Each year, we began the 90 d sampling period with in-water captures post-mating and subsequent beach sampling during the 3 following arribada events. Mating occurs during a discrete period early in the females' nesting season, with males departing when peak female receptivity passes (Plotkin et al. 1996).

2.2. In-water post-mating female sampling

We partnered with the San Juanillo fisherman's association called ASOPESJU, which offers boat rent-

als with an experienced captain for purposes such as fishing, wildlife tours, and scientific research. The community near Ostional and San Juanillo rely on this group for much of the fresh fish for sale in the region. Fishers in ASOPESJU survey the area daily and communicated to us when they began observing mating couples floating at the surface. These daily surveys by ASOPESJU defined the onset of the mating period. Females sampled after intromission are expected to be in an earlier stage of their reproductive cycle than females sampled on the nesting beach already laying eggs. We dedicated the first few weeks of the season to the capture, marking, and sampling of post-mating females (PMFs) in-water using boat surveys from 7:00 to 13:00 h each day. We designated the first day of boat sampling each year as Day 0 for timeline analyses. We launched the boat from San Juanillo, Guanacaste, Costa Rica, and then drove south to waters about 2—4 km off the coast of Ostional beach, where males and females accumulate for mating prior to mass-nesting (Plotkin et al. 1996, Pandav et al. 2000). Scouts identified mating couples floating at the surface. After we confirmed that intromission between the male and female was complete, we hand-captured couples and transferred them onto the boat for ultrasound examination and body morphometrics. We used ultrasound imaging of the oviduct and ovaries to determine the reproductive stage of each female and imaged the subcutaneous fat layer in the dorsal shoulder region for measurement of its thickness. We collected data for body mass and curved carapace length (CCL) for body condition estimations. Turtles were tagged with Inconel No. 691 flipper tags (National Band & Tagging Company) and released right after examination.

2.3. Arribada nesting sampling

Nesting turtles examined during arribadas include females who had not been previously sampled ('new arribada') and females previously sampled in-water, post-mating or during a prior nesting event that same year ('recaptured arribada', identified by flipper tags). The first arribadas of the period sampled each year (Arribada 1) occurred in early July (2016) and late July (2017). Subsequent arribadas occurred about 1 mo apart and are designated Arribada 2 and 3. Subsequent arribada aggregations were intensively searched for potential recaptures, as well as new turtles to be sampled. During arribadas, we spread teams out into transects in flexible regions with the highest density of nesting females to improve chances of find-

ing recaptures. We did not disturb nesting females for sampling until they reached the trance-like stage of egg deposition (Dutton 1996), which occurs following completion of the egg chamber after the first few eggs have been deposited. Because olive ridleys are protected, we did not collect data on body mass until after completion of nesting to minimize disturbance and reduce the likelihood of interfering with nest site selection. To calculate egg-adjusted female mass (kg), eggs were counted as they were deposited in the nest using a handheld tally counter. We weighed the first 10 eggs of each clutch (in kg) using a hanging scale and calculated their average weight for reproductive output contrasts. To address whether weighing pre- or post-oviposition mass measurements would impact the BCS estimations, we replicated the statistical test for each of the BCSs with egg-mass-adjusted female body condition using Eq. (1):

$$\text{Egg-adjusted female mass} = \text{Female mass} + (\text{Average egg mass} \times \text{Clutch size}) \quad (1)$$

Clutch mass represented an average of 8.09 ± 2.61% of total body mass, and weighing post-nesting could bias results toward a decline that does not represent overall fat mobilization.

2.4. Ultrasound examinations

To measure SQFT, we used a Vet 180 Plus ultrasound (SonoSite) with C60/5-2 MHz broadband, 60 mm head with curvilinear transducer, and we used a technique previously described and validated using necropsy in leatherbacks *Dermochelys coriacea* (Harris et al. 2016). To control for researcher effect, one researcher (B. L. Myre) performed all SQFT ultrasound examinations. The tissue composition of the shoulder includes hyperechoic structures (bone, fascia), echoic structures (ligaments, tendons, musculature), with fewer options appearing anechoic in this region (subcutaneous fat, air, or fluid pockets). Because we used the head of the humerus as a landmark, we were confident that we were not measuring synovial fluid. We placed the ultrasound probe in a vertical orientation to the shoulder in the axillary acoustic window on the dorsal shoulder, using the glenohumeral joint as a landmark to keep measurement location consistent from turtle to turtle. We obtained 3 sonograms of the anechoic layer (representing fat) deep to the epidermis and dermis: one image about 1 cm medial to the glenohumeral joint, one directly over the joint, and about 1 cm lateral to

the joint (Harris et al. 2016, Pico 2021). All fat measurements were taken at a depth of 4.9 cm to facilitate image comparison. Examples of these images are shown in Fig. 1E,F. We averaged these 3 measurements to obtain SQFT. Following shoulder imaging, we performed ultrasound examinations of the gonads for the reproductive staging of each female and measurements of ovarian follicle diameter (Rostal et al. 1990). Following completion of the nesting season, we uploaded coded sonograms (to obscure when females

were examined) to avoid bias, then distributed the images randomly to assistants for digital measurement. The ImageJ digital image analysis package (National Institutes of Health, Bethesda, MD) was used to take diameter measurements. To control for variability between individuals, each assistant was first trained by taking measurements from specific structures. Then, B. L. Myre took measurements of reproductive structures on a set of 30 sonograms and asked for assistants to measure the same structures.
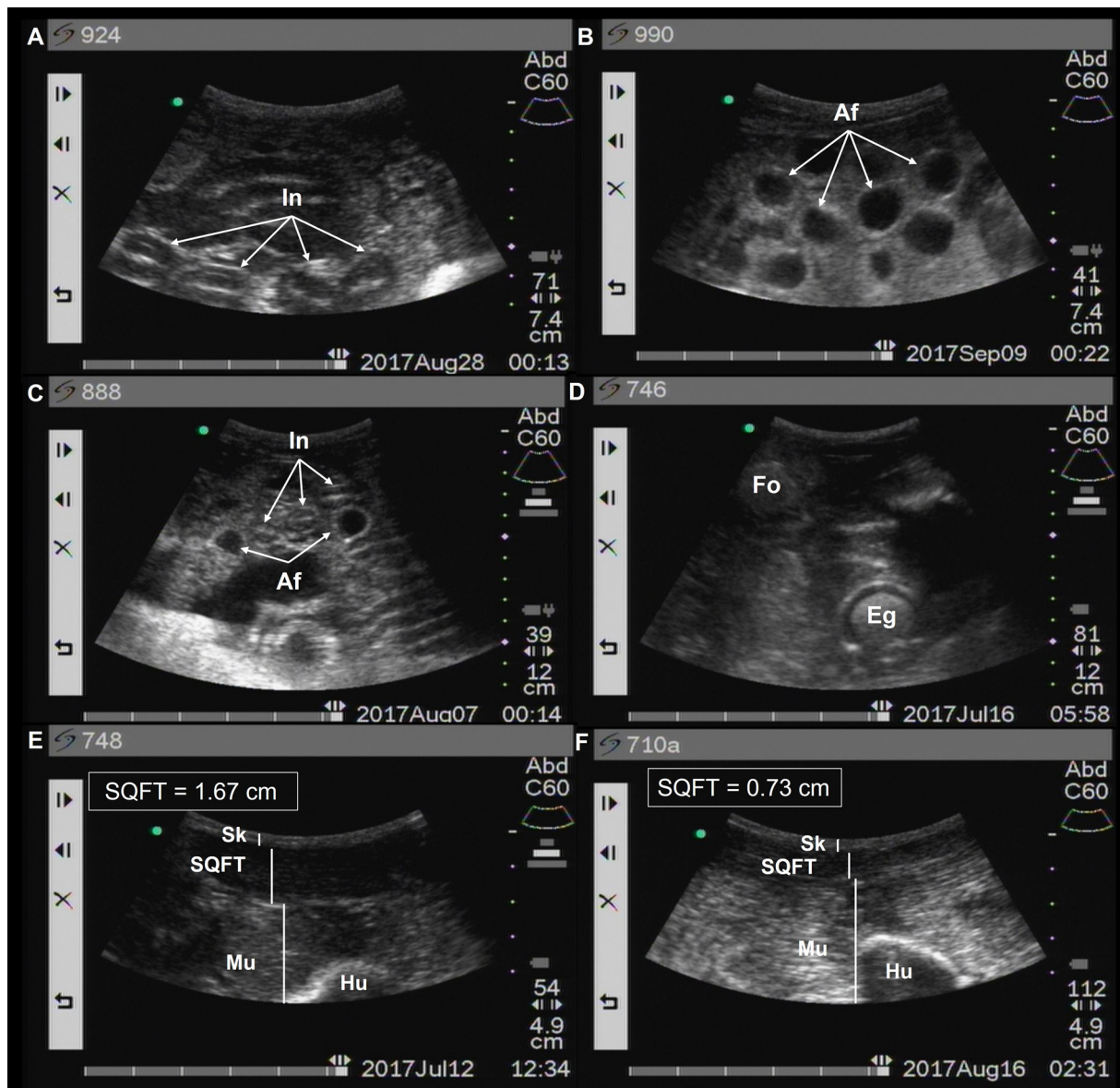

Fig. 1. Sonograms depict example structures of interest for (A−D) reproductive classification and (E−F) subcutaneous fat thickness (SQFT) measurement. (A) Visualization of loops of distal intestine (In). (B) Sonogram from a female with multiple atretic follicles (Af) present. (C) Example sonogram showing Af and intestine with contents (In). (D) Examples of a developing follicle (Fo) and a shelled egg in the oviduct (Eg). (E) Subcutaneous fat layer ultrasound showing epidermis and dermis (Sk), with a thick (E) and thin (F) sub-cutaneous fat layer thickness (SQFT), skeletal muscle (Mu), with the head of the humerus (Hu) shown as a landmark

Only the measurements of the assistants that achieved a Pearson correlation coefficient of >98% with B. L. Myre were employed in the final data analysis. When present, we selected 5 vitellogenic follicles and 5 egg yolks visible within calcified eggshells from each female for measurement (based on image clarity) and averaged for reproductive output contrasts. We also carefully checked each gonadal ultrasound image for evidence of contents in the intestine, suggesting recent feeding. We determined presence of intestinal contents in the prefemoral window by looking for a hyperechoic line with an additional echoic layer surrounding it (Fig. 1A,C). We looked for 3 or more of these structures near one another to avoid false positives due to the similarity of the ovoid shape of the kidney. The external circle was also composed of multiple layers, representing the intestinal wall. We were able to easily distinguish intestinal loops from other reproductive structures such as eggs because the egg yolk appears as a sphere on ultrasound and had an average diameter of 3.07 ± 0.122 cm (Fig. 1D) whereas atretic follicles are distinct due to their anechoic center (Fig. 1B,C).

To determine if body condition indices reflected mobilization of stored resources over the nesting season, we chose 3 ways of classifying females. Initially, we used day of sampling to evaluate changes over time. However, for females sampled for the first time during an arribada, the sampling day does not reflect the progression within an individual female's reproductive cycle, because females migrate independently of one another (Plotkin et al. 1996). Therefore, we re-classified all females by ovarian state based on our sonograms to determine whether each female was showing signs of atresia, representing ovarian regression, indicating she is preparing to return to feeding grounds and is late in her individual nesting season or, potentially, indicating poor nutrition. During atresia, females resorb vitellogenin from ovarian follicles prior to initiation of remigration to foraging areas. We classified females with visible vitellogenic follicles and no atretic follicles as 'non-atretic/early nesting' and females with no visible vitellogenic follicles and/or visible atretic follicles were classified as 'atretic/late nesting,' meaning the female is preparing to return to foraging areas. Finally, we compared initial BCS and SQFT to recaptured BCS and SQFT in the subset of samples for which we were able to obtain an initial sample at post-mating or during a nesting event and a recapture sample of the same tagged turtle at a subsequent nesting event. Recaptures were relatively rare despite high sampling effort (19.7% of all PMFs sampled).

2.5. Body condition scores

Most studies calculate BCS using straight carapace length (SCL; cm). We were only able to collect CCL data, so we calculated estimated SCL (eSCL; cm) using a conversion equation used in previous studies on olive ridleys (Eq. 2) (Whiting et al. 2007, Petitet et al. 2015). We then used eSCL in BCS calculations.

$$eSCL = (0.818 \times CCL) + 9.244 \qquad (2)$$

We first used FCF for BCS, which was calculated by inputting the mass (kg) and eSCL data into the Fulton's factor formula (Eq. 3). FCF has been widely used for measuring body condition in sea turtles (Bjorndal 1985, Seminoff et al. 2004, Keller et al. 2005, Clukey et al. 2017, Lamont & Johnson 2021).

$$FCF = 10000\left(\frac{Mass}{Length^3}\right) \qquad (3)$$

Because previous studies have shown that FCF calculation occasionally fails to detect expected shifts in body condition (Rossi et al. 2019), a more sensitive body condition score, K_{rel}, was calculated (Labrada-Martagon et al. 2014), modified from Le Cren (1951). To calculate K_{rel}, we first used the log-transformed equation to estimate parameters a and b (Eq. 5). All individuals were pooled to estimate a and b.

$$Mass = aSCL^b$$
$$\rightarrow \log(Mass) = \log(a) + b\log(SCL) \qquad (4)$$

The slope of the regression is the population-specific allometric growth parameter b (this parameter is assumed to be 3 in FCF calculations due to Galileo's cube law), which represents the weight gained for each unit of length increased. The y-intercept of this line is $\log(a)$, where a is a population-specific adjustment for body condition factor. The parameter a was estimated by $10^{\log(a)}$ to undo the log transformation. Once a and b were estimated, we used them to generate K_{rel} for each turtle.

$$K_{rel} = \frac{1000 \times Mass}{aLength^b} \qquad (5)$$

2.6. Statistics

We used JMP 16 (JMP®, version 16, SAS Institute) and R (https://www.R-project.org) for statistical analyses. *A priori* power analysis indicated a sample size of 30 per contrast would allow for detection of significant differences, and this goal was met for all analyses. We tested all parameters for normality with a Shapiro-Wilk test and homogeneity with Levene's

test prior to contrasts. To meet these assumptions, we log-transformed SQFT prior to analysis. All other parameters were normal and homogeneous. Our first statistical objective was to determine if measured variables significantly changed over sampling day, ovarian state, or between initial capture and recapture. To determine if FCF, K_{rel}, or SQFT changed over the sampling season, we ran an ANOVA adjusted for repeated measures to compare means of initial captures versus recaptured samples (2−6 wk apart). We then ran 2 ANOVAs to compare the means of FCF, K_{rel}, and SQFT for turtles grouped into early or late season by behavioral state (PMF vs. arribada nesting, A) and ovarian state (non-atretic or early nesting vs. atretic or late nesting). When ANOVAs indicated a significant difference, we then used Tukey's HSD post hoc tests for pairwise comparisons.

We calculated FCF and K_{rel} using post-nesting female mass and egg-adjusted female mass to see if accounting for the clutch itself would change the interpretation of BCS contrasts. To compare the stored resources of initial captures versus recaptured turtles, we ran an ANOVA adjusted for repeated measures for BCS and SQFT of any females captured 2−3 times per season. $p < 0.05$ was considered significant for all analyses except for the χ^2 test for frequency of detected intestinal contents in which $p < 0.01$ was considered significant.

3. RESULTS

Over both seasons, we were able to sample a total of 123 post-mating and arribada nesting turtles (Table 1). We tested for variation in all metrics (egg number, egg mass, estimated straight carapace length, body mass, BCSs, and SQFT) by contrasting them by day of

arribada sampled (example: Day 1 vs. Day 5). We also contrasted the same metrics for differences in the month of arribada nesting female sampled (example: July arribada vs. September arribada) and found no differences in any metric, so we pooled all A females into 1 category for behavioral state (mating or A) contrasts. We sorted females into categories for contrasting BCSs and SQFT: behavioral state (PMF n = 59, A n = 64), ovarian state (early n = 46, late n = 74), and recapture (n = 12). The initial versus recapture data represent a subset of turtles sampled 2 (n = 9) to 3 times (n = 2) in 1 season and are the only contrast done within the same individuals over a known number of days. Overall, body mass, carapace length, and SQFT did not differ over time within any of the categories. FCF ($F_{(1,121)}$ = 15.87, p = 0.0001, and K_{rel} $F_{(1,121)}$ = 18.66, p = 0.0001), declined significantly from post-mating to nesting, but this effect was reversed when female mass was adjusted for egg mass (Table 1, Fig. 2). FCF and K_{rel} did not change with ovarian state or from initial capture to recapture and showed no significant year effect.

SQFT did not significantly differ between the post-mating and nesting samples. Likewise, we found no significant difference in log-transformed SQFT for early (non-atretic) and late (atretic) ovarian state. We found no significant differences in BCSs between atretic and non-atretic females.

For animals sampled more than once in a single season (recaptures), mean FCF and K_{rel} did not change from initial capture sample to recapture sample. Mean SQFT also did not significantly differ between initial capture and second capture.

Because these recaptures represented the only turtles in which the number of days between samplings was precisely known, they provided an opportunity to examine stored resource changes over time. To

Table 1. Summary of field sampling data and derived body condition scores. Classifications indicate the 3 different ways turtles were classified for analysis: reproductive behavior state, ovarian state, and recaptures. CCL: curved carapace length; eSCL: estimated straight carapace length; SQFT: subcutaneous fat layer thickness; FCF: Fulton's condition factor; K_{rel}: relative body condition. Values are means ± SE. *p < 0.05

|	N (total females sampled)	Mean CCL (cm)	Mean eSCL (cm)	SQFT (cm)	Mass (kg)	FCF	K_{rel}
Post-mating females	59	66.98 ± 0.38	65.07 ± 0.33	0.93 ± 0.07	41.18 ± 0.66	1.49 ± 0.01	5.74 ± 0.05
Arribada females	64	66.15 ± 0.38	63.35 ± 0.31	0.76 ± 0.02	36.00 ± 0.60*	1.41 ± 0.02*	5.41 ± 0.05*
Arribada females (egg adjusted)	64	66.15 ± 0.38	63.35 ± 0.31	0.76 ± 0.09	38.92 ± 0.65	1.53 ± 0.02	5.85 ± 0.06
Ovary early	46	66.98 ± 0.41	64.21 ± 0.35	0.80 ± 0.05	38.95 ± 0.86	1.46 ± 0.02	5.73 ± 0.13
Ovary late	74	66.74 ± 0.39	64.03 ± 0.33	0.81 ± 0.04	38.16 ± 0.63	1.45 ± 0.01	5.89 ± 0.07
Initial capture	12	66.78 ± 0.83	63.87 ± 0.68	0.83 ± 0.07	39.60 ± 1.88	1.51 ± 0.04	5.81 ± 0.17
Recapture	12	66.78 ± 0.83	63.87 ± 0.68	0.70 ± 0.06*	37.60 ± 1.40	1.44 ± 0.04	5.54 ± 0.16
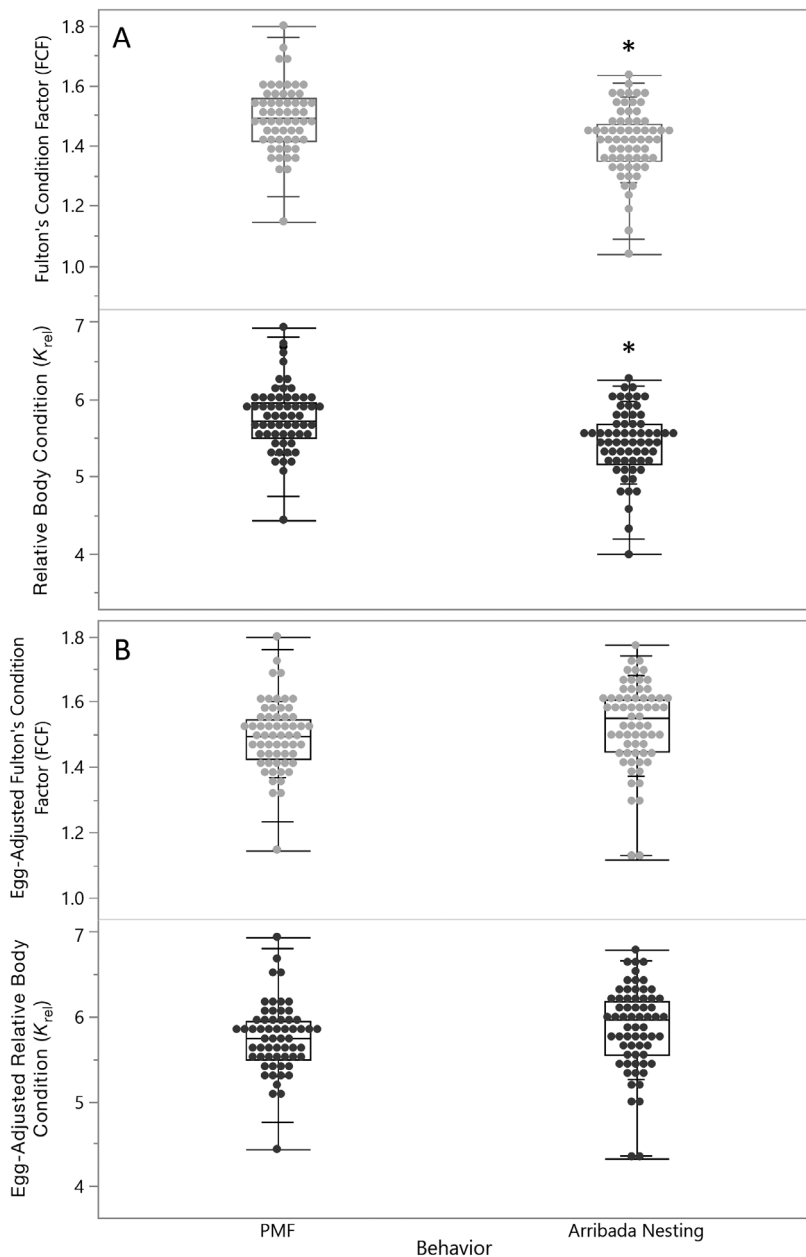
Fig. 2. Adjusting for egg mass changes trends in Fulton's condition factor (FCF) and relative body condition (K_{rel}) from post-mating to nesting. (A) Total mass, FCF and K_{rel} both significantly decline from post-mating to nesting. (B) Adjusted for egg mass, FCF and K_{rel} did not change between post-mating and nesting. Box plots: interquartile range with center line representing the median; upper and lower whiskers: range. Asterisks: statistically significant (p < 0.05) differences between post-mating and arribada nesting; dots: individual turtle body condition scores. PMF: post-mating females

examine this, we plotted each value against days of the sampling interval (Fig. 3). For all recaptures (n = 12), no significant difference in mean BCSs were detected by date or between years (Table 2).

We found no significant differences in FCF, K_{rel}, or SQFT by ovarian state (Table 2). We found that the non-egg corrected values for FCF ($F_{3,121}$ = 14.574, p < 0.0001) and K_{rel} ($F_{3,121}$ = 11.976, p < 0.0001) significantly declined from post-mating to nesting in both years. When adjusted for egg mass, FCF and K_{rel} did not significantly change from mating to nesting (Table 2).

When log-transformed SQFT values were regressed against sampling day, we found no significant change in SQFT over time in any recaptures from 2017 (n = 7) but a significant decline from initial capture to recapture in 2016 (Fig. 3). Females in 2016 had more stored fat at the beginning of the season than in 2017, as determined by the t-test ($t_{(9)}$ = 5.951, p = 0.0002). To determine whether BCS reflected stored fat, we regressed SQFT against 2 BCSs and found no significant correlation.

We also detected no significant differences in reproductive output as measured by ultrasound follicle diameter, clutch size, or egg mass (Table 3). There was no significant difference in frequency of intestinal contents between group-wise comparison, except for between 2016 and 2017 (n = 99, df = 1, χ^2 = 8.98, p < 0.01).

4. DISCUSSION

The olive ridley sea turtle is the most abundant sea turtle in the world (Abreu-Grobois & Plotkin 2012), but in some ways, the least understood. This species has an evolutionary history divergent from other sea turtles. Olive ridleys are the only pelagic chelonid (Plotkin 2003). They also lack migratory corridors and commonly revisited feeding areas, which allows for a high degree of flexibility in migration and opportunism in foraging decisions. As the smallest-bodied genus of sea turtle, ridleys are likely physically not able to store as much fat as larger species. As a result, they may use available feeding areas near their nesting beaches to supplement any stored capital (energy reserves) obtained prior to the reproductive migration. Ridleys also differ from other sea turtles because they breed annually instead of taking recovery years between
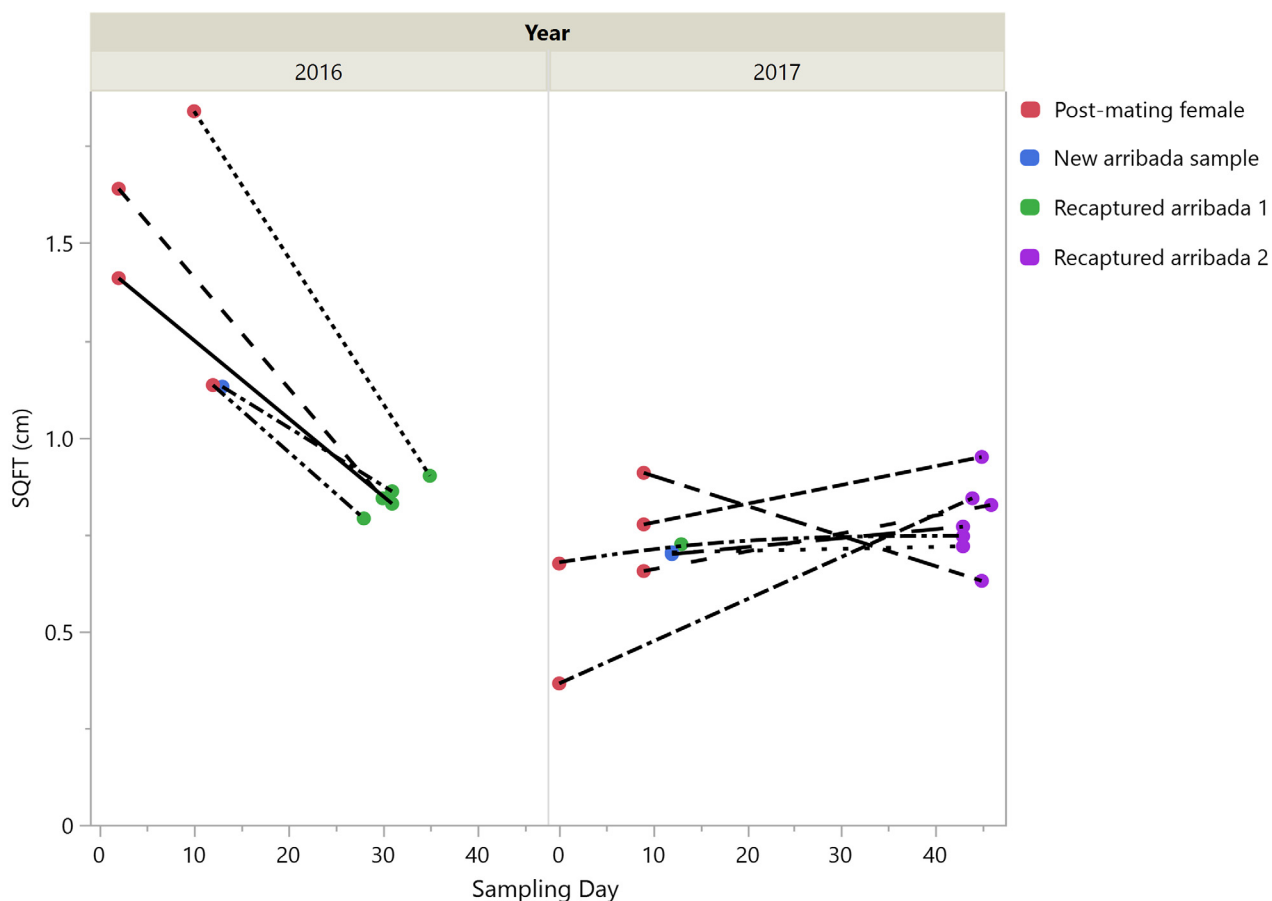
Fig. 3. In 2016, subcutaneous fat thickness (SQFT) decreased over the season while it did not in 2017. Initial and recapture SQFT for females captured twice in a reproductive year by year sampled

reproductive seasons. This is significant as they do not have an 8–10 mo period available prior to their reproductive migrations to produce yolk proteins and sequester them into hundreds of oocytes as observed in other sea turtle species (Wibbels et al. 1990). We propose that olive ridleys represent an intermediate, neither a purely capital nor income, breeding strategy because they have abundant food available near their

breeding and nesting areas, have shorter remigration intervals and lower overall annual reproductive output than larger-bodied capital breeding sea turtles. The capital–income breeding continuum is defined by an organism's use of food resources at breeding grounds to ensure reproductive success. This use ranges from low (capital) to high (income). If olive ridleys are intermediate breeders, then a non-invasive way to

Table 2. Summary of comparison by year within each classification, explained in Table 1. Data are mean ± SE; values in parentheses give n only when it is different from N. SQFT: subcutaneous fat thickness; FCF: Fulton's condition factor; K_{rel}: relative body condition. *p < 0.05

	Total N	SQFT		FCF		K_{rel}	
		2016	2017	2016	2017	2016	2017
Post-mating females	59	1.00 ± 0.09 (25)	0.69 ± 0.06 (8)	1.47 ± 0.02 (29)	1.51 ± 0.01 (30)	5.67 ± 0.09 (29)	5.80 ± 0.05 (30)
Arribada females	64	0.76 ± 0.04* (30)	0.76 ± 0.02 (34)	1.37 ± 0.02 (30)	1.45 ± 0.01 (34)	5.26 ± 0.09 (30)	5.54 ± 0.05 (34)
Ovary early	46	0.83 ± 0.07 (19)	0.76 ± 0.05 (10)	1.41 ± 0.03 (20)	1.51 ± 0.01 (26)	5.42 ± 0. 14 (20)	5.78 ± 0.06 (26)
Ovary late	74	0.89 ± 0.06 (36)	0.74 ± 0.03 (32)	1.44 ± 0.02 (36)	1.46 ± 0.01 (38)	5.53 ± 0.08 (36)	5.58 ± 0.05 (38)
Initial capture	12	1.43 ± 0.14 (5)	0.69 ± 0.07 (7)	1.43 ± 0.26 (2)	1.54 ± 0.02 (8)	5.52 ± 1.03 (2)	5.88 ± 0.07 (8)
Recapture	12	0.84 ± 0.02* (5)	0.76 ± 0.03 (7)	1.35 ± 0.22 (2)	1.47 ± 0.03 (8)	5.20 ± 0.84 (2)	5.62 ± 0.11 (8)

Table 3. Reproductive output of female olive ridleys as measured by follicle size, clutch size, and individual egg mass; no significant differences were found by year. 2016 was the year of the strong El Niño Southern Oscillation event; 2017 was a recovery year with La Niña starting after the field season. Parentheses denote n; values are means ± SE. X: measurements not applicable for post-mating females. *p < 0.05

	Total N	Follicle diameter (cm)		Clutch size		Egg mass (g)		Frequency of contents found in intestine	
		2016	2017	2016	2017	2016	2017	2016	2017
Post-mating females	59	2.40 ± 0.06 (20)	2.22 ± 0.04 (6)	X	X	X	X	6/13	16/31*
Arribada females	64	2.60 ± 0.06 (29)	2.41 ± 0.04 (31)	97.62 ± 4.06 (32)	98.88 ± 3.29 (34)	33.04 ± 0.53 (29)	31.24 ± 0.31 (34)	11/28	22/27*
Ovary early	46	2.54 ± 0.09 (15)	2.39 ± 0.10 (8)	92.18 ± 6.13 (11)	103.80 ± 7.13 (5)	32.53 ± 0.90 (11)	31.40 ± 0.40 (5)	9/18	7/14
Ovary late	74	2.51 ± 0.05 (36)	2.38 ± 0.04 (38)	102.7 ± 4.99 (20)	98.03 ± 3.67 (29)	33.73 ± 0.62 (18)	31.22 ± 0.36 (29)	14/23	31/44

estimate energy balance is needed. If available, it would allow for assessing whether female energetic needs are being met at this important life stage. Our data indicate that olive ridleys have the flexibility to feed actively during the nesting season following strong ENSO events and, with appropriate resources available, are highly resilient and able to maintain their reproductive output despite adversity. Our sample size for years sampled is very low, but these 2 years, in particular, represented an important opportunity for contrast of nutritive state and reproductive output. The differences found in resource use patterns indicate that longer term studies are needed to establish baseline physiological parameters. Our data evaluating reproductive output and strategy, the first for olive ridleys, contrast with the lower reproductive output seen following ENSO events in other species (Saba et al. 2007, Previtali et al. 2010, Ancona et al. 2011, Saragoça Bruno et al. 2020). Despite this reproductive resilience, this species requires rigorous and innovative protection, as the International Union for the Conservation of Nature (IUCN) has classified it as Vulnerable due to a steep population decline of 30–50% in recent years (Abreu-Grobois & Plotkin 2012, Cáceres-Farias et al. 2022).

Capital breeding animals should mobilize stored lipid in preparation for the first nest; we found this pattern in 2016, when SQFT significantly declined between initial measurement and recapture in all 5 individuals, which may indicate that olive ridleys use a capital strategy when availability of prey at the nesting grounds is reduced following prolonged ENSO events. In contrast, in 2017, SQFT did not significantly change according to behavioral state (mating or nesting), ovarian state (early or late), or from initial measurement to recapture, demonstrating that subcutaneous lipid stores were not the primary energy source used for egg production in those individuals. This suggests that olive ridleys feed adjacent to their breeding and nesting grounds to support egg production, as supported by the higher incidence of visible contents in the adjacent intestines for that year. Despite lesser use of fat stores in 2017, egg number and weight did not change. However, we were unable to monitor the entire beach between arribadas, so we cannot say if females laid a different number of clutches. We also did not measure oviductal fluid released with the eggs, and so this may have added variability to egg-adjusted contrasts. The need for a reliable, non-invasive metric to quantify energy balance in an organism is illustrated by the lack of consensus on a calculation technique (Morton & Routledge 2006, Plăiaşu et al. 2010, Zweig 2014). FCF and

K_{rel} showed no significant difference in females contrasted by ovarian state, implying that females are not losing significant mass on average before the onset of ovarian regression. While BCSs declined from post-mating to nesting, this effect was reversed when we adjusted for egg mass, indicating that the significant decline was due to a loss of weight due to oviposition and not due to fat mobilization. While a few studies have found significant correlation between BCS and subcutaneous fat measurements in large mammals (Dechow et al. 2002, Ayres et al. 2009, Alapati et al. 2010) and snakes (Waye & Mason 2008), this was not the case in this study, as the 2 tested techniques for BCS calculation showed no correlation with SQFT. These results indicate that the high variability of female weight during the nesting season can make weight–length ratios hard to interpret in olive ridley sea turtles. When the whole of these results is considered, olive ridley sea turtles exhibit many income-like characteristics. This demonstrates a departure from the expected capital breeding pattern, which would show significant declines in body mass, including fat, for egg production from beginning to end of each season. Prior to development of ultrasound subcutaneous fat measurement, BCSs have been frequently used as a proxy for body composition or adiposity. We found that SQFT was the more useful metric than BCSs due to the contrasts that could be drawn based on the year effect when FCF and K_{rel} contrasts showed no significant difference.

A need for a non-destructive, direct measurement of adipose tissue has driven development of ultrasound techniques across diverse taxa. For example, ultrasound subcutaneous fat measurement has been applied to anatids (Sears 1988), pinnipeds (Field et al. 2005, Mellish et al. 2007), humans (Wagner et al. 2019), sheep (Leeds et al. 2008), bovids (Schröder & Staufenbiel 2006, Alapati et al. 2010), and right whales (Moore et al. 2001). This measurement quantifies a physical layer of lipid deposited under the skin, which can be monitored over time as an indicator of fat storage or mobilization. Prior to development of this technique, BCSs have been frequently used as a proxy for body composition or adiposity in sea turtles. Measurement of SQFT using ultrasound was a fast and relatively non-invasive procedure that should be easily applied to any sea turtle. To get an accurate measurement, it is important to ensure the flipper of the turtle is at a neutral, 45° angle to reduce compression on the lipid layer from surrounding skin and musculature, and taking 3 measurements around the glenohumeral joint and calculating an average allows for consistency in the metrics.

We set out to determine if we could find evidence that olive ridleys maintain their subcutaneous lipid layer from post-mating to nesting and found that axillary SQFT did not change in most contrasts. In 97 turtles examined, SQFT ranged from 0.32–1.23 cm, expectedly smaller than that reported for leatherbacks *Dermochelys coriacea* (Harris et al. 2016), facultative endotherms which use their subcutaneous fat layer both for thermoregulation and an energy storage site in temperate regions (Wallace & Jones 2008, Davenport et al. 2009). Tropical species such as the olive ridley have little need for insulation and use intraperitoneal fat as the primary site for lipid mobilization during egg production (Kwan 1994, Hamann et al. 2002). Ultrasound measurement of SQFT therefore should be validated before this technique is more widely applied. Despite multi-year efforts in both Texas, USA, and Costa Rica, our team was not able to access *Lepidochelys* carcasses to perform shoulder dissection and histology to confirm our measurements as fat; it would greatly benefit the field to perform this validation. While we were unable to validate this technique in our species using necropsy, a recent study conducted successful necropsy validations in green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles (Pico 2021). If the subcutaneous fat layer has no storage function for ridleys, then we would not expect to detect differences across repeated samples, making the decline of SQFT in 2016 interesting. Perhaps these females depleted their intraperitoneal options and then drew from alternate peripheral stores. Further investigation using blood metrics of fat mobilization may further clarify whether this species mobilizes intraperitoneal or hepatic fat, or liver glycogen for energy during nesting, particularly in challenging years. Critter cams and assays for hormones impacted by feeding could also be used to assess feeding behavior during the nesting period.

The unexpectedly low frequency of non-atretic/early females (46 early/non-atretic vs. 74 late/atretic) may also imply that female olive ridleys can select follicles for reabsorption in the migratory or mating periods, as only 38% of post-mating females examined were classified as non-atretic/early. In 2017, females showed no significant difference in SQFT despite having a longer period (~10 d more) between initial and recapture compared to 2016. The 2017 SQFT recapture by sampling day showed that females were not mobilizing significant SQFT during periods of egg production, and the behavioral state contrast showed no significant difference in SQFT between post-mating and nesting or by ovarian state. Together, these results give evidence of income breeding characteristics in olive rid-

leys during years of resource abundance. We found significantly more presence of intestinal contents in 2017 regardless of whether the female was a recent arrival to the nesting beach and sampled post-mating or had been at the nesting grounds for at least 2 wk and sampled at nesting. Diets of olive ridley turtles can vary widely and include snails, fish, mollusks, crustaceans, jellyfish, and tunicates (Bjorndal 1997). Not all of these food items have large calcium deposits likely to be hyperechoic on ultrasound, so the frequency of intestinal contents could be underestimated. Gut transit studies have not presently been conducted in olive ridleys, but the Kemp's ridley has been estimated to pass lobster shell out of the gut in 7–8 d (Burke et al. 1994), with larger sea turtle species passing indigestible markers in a wide range of transit times from 1–5 wk. For loggerheads gut transit ranged 8–40 d (Di Bello et al. 2006, Valente et al. 2008, Manire et al. 2017) and for greens it ranged 7–35 d (Brand et al. 1999, Amorocho & Reina 2008, Manire et al. 2008). Given these estimates, a 90 d sampling period should be sufficient to see a drop in the number of females with intestinal contents obtained at feeding grounds by halfway through the nesting season. The higher frequency of intestinal contents throughout sampling suggests that more females actively fed during the nesting season, perhaps to assist in maintaining reproductive output during a nesting season with low resource stockpiling, as indicated by initial SQFT, or for recovery from a strong ENSO event.

Though olive ridleys are part of a family of mostly capital breeders (Cheloniidae), other animal families have shown diversity in breeding strategy. Evidence for diversity in breeding strategy among related species has been shown to be driven by environmental conditions and resource availability (Wheatley et al. 2008). For example, within anatids there is a rich diversity of breeding strategies from opposite ends of the spectrum. Extreme capital breeders in this family include the Brent goose *Branta bernicla*, in which resources acquired prior to breeding are so critical that body condition at stopover areas on the breeding migration directly correlates to reproductive success measured months later (Ebbinge & Spaans 1989). In contrast, most ducks are income breeders who must have adequate access to resources near the nesting grounds for reproductive success (Bond et al. 2007). But as our understanding expands on what drives these life history strategies on the extreme ends of the spectrum, of increasing scientific interest are the more subtle shifts occurring in species using an intermediate breeding strategy (Evans & Bearhop 2022). For example, greater snow geese *Anser caerulescens*

have been proposed to be an intermediate capital—income breeder due to the finding that stable isotope deposition into the egg yolk contained signatures derived from both the feeding ground and the nesting area (Gauthier et al. 2003). The timing of feeding in relation to migration is a key factor in determining where an organism sits on this continuum. The olive ridley seems to exhibit an intermediate strategy most like peregrine falcons *Falco peregrinus tundrius*. Peregrine falcons stockpile nutritional resources during reproductive inactivity prior to migration but also feed post-migration once they arrive at nesting grounds, where males present females with food as part of courtship. Olive ridleys appear to exhibit a similarly opportunistic strategy, using both stored resources and concurrent food intake to drive reproduction.

In species which fall into the intermediate breeding group, there may be more flexibility for adaptation to varying environmental conditions, and in a world of increasing environmental stochasticity, organisms that can modify their physiology and behavior in response to environmental change are more likely to reproduce successfully (Evans & Bearhop 2022). This has been documented in reptiles. For example, the aquatic snake *Seminatrix pygaea*, a typically capital-breeding species, was documented to use income breeding to reproduce following a prolonged, severe drought in which nutritive resources were devoid (Winne et al. 2006). This strategy was largely credited for why this species showed unchanging reproductive output regardless of drought conditions, which can lead to much lower reproductive success in species like the water python *Liasis fuscus* (Shine & Madsen 1997, Madsen & Shine 2000) that does not switch between strategies. In contrast, female aspic vipers *Vipera aspis* can use stored energy to reproduce in seasons when they have failed to catch a single prey item (Lourdais et al. 2003), allowing for reproduction despite extremely low resource availability. This contrast implies that flexibility between strategies, rather than the strategy itself, may allow for resilience in a rapidly changing climate. Perhaps the shifts observed in the year effect for SQFT indicate a similar flexibility in olive ridleys, especially considering the climatic shifts which occurred between these 2 sampling seasons.

Over the past century, anthropogenic carbon emissions have driven ever-escalating climatic events, and earth temperatures have been documented to increase with the establishment of industrialized human society. The strongest example of a natural inter-annual climate fluctuation is the ENSO, which allows for observation of a population's response to increasing oceanic temperatures as well as observation of the recovery

that may or may not occur during the following La Niña event. ENSO events have been projected to increase in frequency as greenhouse-gas concentrations in the atmosphere continue to increase (Timmermann et al. 1999), so documentation of any physiological or behavioral shifts that may occur during the La Niña event (2017) may be useful as guides for supportive management plans to assist recovery in olive ridleys.

Traditionally, sea turtles have been considered capital breeders, but factors which have driven other sea turtle species toward capital breeding have been lost in the olive ridley. The ETP olive ridleys nest near a marine biodiversity hotspot known as the Costa Rican Thermal Dome. This rich nutritional resource so close to nesting beaches makes for ideal conditions for concurrent feeding during the nesting season, and females may utilize this resource more during years of resource restriction at feeding areas. The upwelling that occurs along the entire eastern Pacific coast drives the deeper cold nutrient-rich water up towards the surface. During ENSO, this cold water at the surface is displaced by warmer water and prey availability is reduced. The high productivity in this area allows olive ridleys in this region to occupy a higher trophic position than other Central American populations (Peavey et al. 2017). Our results support this, as following the strong ENSO year, recaptured arribada nesting females showed a significant decline in SQFT, but not in the subsequent La Niña year. This may indicate that the increased availability of prey at the nesting grounds did not necessitate fasting and fat mobilization during nesting. The flexibility of breeding strategy in the olive ridleys perhaps allowed for no change in reproductive output despite significant environmental shifts, a resilience not yet observed in other sea turtles. The unique, and highly flexible nature of migratory and feeding decisions in this species may account for some of the reasons that this species has been so successful and abundant historically.

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