Blood oxygen stores of olive ridley sea turtles, *Lepidochelys olivacea* are highly

variable among individuals during arribada nesting

by

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ABSTRACT

Sea turtles are mostly pelagic, air-breathing divers that can become neritic during nesting season. Sea turtles dive with a full lung of air and these O_2 stores are supplemented by O_2 stored in blood. Olive ridley sea turtles exhibit polymorphic nesting behavior; mass nesting behavior called arribada, where up to 25,000 turtles will nest at once, and solitary nesting behavior. As mostly pelagic and highly migratory species, we hypothesize that newly arrived turtles, nesting in arribadas, will exhibit increased blood oxygen stores as compared to solitary nesting towards the end of the season, where turtles have likely become neritic. We measured blood volume and associated variables to estimate total blood O_2 stores including hematocrit and blood hemoglobin content. There were no significant differences in mean values between nesting periods, but arribada nesting individuals were more variable than those performing solitary nesting. Mass specific plasma volume was relatively invariant among individuals but mass specific blood volume and blood oxygen stores varied widely, 2-fold and 3-fold, respectively. Blood O_2 stores represented 32% of total body O_2 stores. Under typical mean diving conditions of 26°C and high levels of activity, blood stores confer ~14 min to aerobic dive times and are likely critical for the long duration, deep diving exhibited by the species. Individual differences in blood O_2 stores strongly impact estimated aerobic dive limits and may constrain the ability of individuals to respond to changes on ocean climate.

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INTRODUCTION

Air-breathing diving animals display a variety of anatomical, physiological, and behavioral adaptations that allows them to increase their time underwater used for foraging, migrating, mating and predator avoidance. These animals maximize time at depth through the use of aerobic metabolism and enhance dive durations through increased body O_2 stores (Kooyman, 1989; Ponganis, 2011; Ponganis & Williams, 2016). Total body O_2 stores are dependent on several variables, including diving lung volume, blood volume, hemoglobin (Hb) concentration, muscle mass, and myoglobin (Mb) concentration (Ponganis & Williams, 2016). While extensive research has been done on O_2 stores and the physiology of breath-hold diving in endotherms, less is known about individual and inter-specific variation in diving O_2 stores in marine reptiles, including sea turtles (Berkson, 1966; McMahon, Bradshaw, & Hays, 2007; Wells & Baldwin, 1994).

Sea turtles are important apex predators in marine ecosystems and have complex predator-prey interactions that help shape food webs. Additionally, sea turtles play important roles in almost every ocean ecosystem, from nesting beaches, internesting habitats, epipelagic habitats, and benthic habitats (Hawkes, Broderick, Godfrey, & Godley, 2009; Heithaus, 2013; Spotila, 2004; Wallace et al., 2011). Out of the five main hazards for marine turtles (climate change, fisheries bycatch, take, coastal development, pollution and pathogens), fisheries bycatch is the biggest threat, followed closely by impacts of climate change (Wallace et al., 2011). Understanding the factors that limit sea turtle breath-hold capacity is important to predicting their ability to respond to potential changes in water temperature and prey distributions that result

from climate change (Yang et al., 2019) and the potential for mortality due to incidental

by-catch in fishing nets, the main anthropogenic threat to sea turtles (Lewison et al.,

2013; Polovina et al., 2004; Polovina, Howell, & Balazs, 2003; Wallace et al., 2011;

Williard, 2013; Yang et al., 2019).

The diving and movement behaviors of free-ranging sea turtles have been well

investigated using data loggers and satellite telemetry (e.g. Arendt et al., 2012;

Bradshaw, McMahon, & Hays, 2007; Ceriani, Weishampel, Ehrhart, Mansfield, &

Wunder, 2017; Chambault et al., 2016; Dodge, Galuardi, Miller, & Lutcavage, 2014; Gaos

et al., 2012; Hays & Hawkes, 2018; Hays, Hobson, Metcalfe, Righton, & Sims, 2006;

Hochscheid, 2014; Howell et al., 2010; Okuyama et al., 2012; Polovina et al., 2004;

Polovina, Howell, Parker, & Balazs, 2003; Richardson et al., 2013; Swimmer et al., 2006).

Sea turtles spend about 90% of their time submerged and without breathing (Williard,

2013). Diving time of sea turtles varies with the purpose of their dive (Heithaus, 2013).

Dive duration in internesting turtles increases with depth (e.g. Hays et al., 2000; Hays,

Metcalfe, & Walne, 2004; S. Hochscheid, Godley, Broderick, & Wilson, 1999), especially

during resting dives, where depth is modulated by the volume of inspired air (e.g. Hays

et al., 2004; Minamikawa et al., 2000; Yasuda & Arai, 2009). During active dives, dive

duration is influenced by activity (Okuyama et al., 2012) and strong impacts of activity

levels on rates of oxygen consumption and heart rates have been measured in captivity

(Enstipp et al., 2011; Williams et al., 2019). As ectotherms, body temperature and rates

of oxygen consumption are also influenced by water temperature in the Cheloniidae sea

turtles (Spotila, O'Connor, & Paladino, 1996).

A key difference among marine divers is whether or not they make use of their lung O_2 stores. The deepest divers, including many marine mammals, dive below the depth of lung collapse and prioritize tissue O_2 stores. Some deep divers, like phocid seals, avoid respiratory gas exchange at depth by diving after exhalation (Ponganis & Williams, 2016). Other marine divers, such as sea turtles and penguins dive following inhalation (S. C. Wood, Gatz, & Glass, 1984), and lung oxygen stores are an important component of diving metabolism (McDonald & Ponganis, 2013). In sea turtles, the lung serves as the major oxygen store during diving and limited measurements of tissue oxygen stores have suggested similar values to non-diving vertebrates (Lutz & Bentley, 1985; Lutcavage et al., 1990, 1992; Ponganis, 2015). For this reason, the literature in sea turtles have deemphasized measurements of blood O_2 stores with most published values from small samples, captive animals or juveniles. To our knowledge, data for the calculation of total blood oxygen stores in the sea turtle, olive ridley (*Lepidochelys olivacea*) have not been reported in the literature, except for one small sample (n=2) of blood volume measurements (Thorson, 1968).

One approach to assess the breath-hold capacity of air-breathing divers is the aerobic dive limit (ADL). ADL is an estimation of physiological and energetic constraints on the dive durations of air-breathing diving animals (Costa, Gales, & Goebel, 2001; Ponganis, Meir, & Williams, 2011; Williams, Meir, & Ponganis, 2011). ADL is the maximum amount of time an animal can spend underwater before the product of anaerobic respiration, lactate, rises beyond resting levels in their blood (Butler, 2006; Costa et al., 2001; Kooyman, 1989). However, establishing a direct and precise ADL

value through measurements of blood lactate is difficult to achieve. Therefore, ADL is calculated as cADL, which is the ratio of the total usable amount of oxygen (O_2) stored in the body (O_2 from blood, muscles and lungs) to the diving metabolic rate (energy budget of an animal) (Ponganis et al., 2011; Ponganis & Williams, 2016). Some studies have reported cADL values of sea turtles that use only estimates of lung O_2 store. Highly variable values of cADL have been reported for leatherback (*Dermochelys coriacea*), loggerhead (*Caretta caretta*), flatback (*Natator depressus*) and hawksbill (*Eretmochelys imbricata*) (Hochscheid et al., 2007; Williard, 2013). No cADL estimates have been reported for olive ridley turtles.

Several recent observations suggest the importance of including blood O_2 stores in the consideration of breath-hold ability in sea turtles (Chambault et al., 2016; Hochscheid et al., 2007; McMahon et al., 2007; Wells & Baldwin, 1994)**.** Biologging data have revealed deep, long duration dives in some species that may exceed the capacity of lung O_2 stores to support aerobic metabolism (Chambault et al., 2016; McMahon et al., 2007). Lung collapse may occur in deep diving turtles due to their compliant respiratory system on the deepest dives evident in biologging studies (Lutcavage, Lutz, & Baier, 1989; Tenney, Bartlett, Farber, & Remmers, 1974). Together, these findings suggest that contribution of tissue O_2 stores to aerobic limits may be critical for some dives. Further, recent studies on the sympathetic autonomic control of pulmonary shunts to limit decompression injuries in sea turtles may limit access to lung O_2 stores in some contexts and the lung stores are accessed using intermittent perfusion (García-Párraga et al., 2018; Portugues et al., 2018).

Olive ridley turtles exhibit two types of nesting behavior, solitary nesting and arribada nesting (Spotila, 2004). Solitary nesting occurs throughout the year and females are widely spaced, returning at varying internesting intervals (Pritchard, 2007; Spotila, 2004). During arribada nesting, thousands of females synchronize themselves to nest together, during the third-quarter moon for a 2-7 day arribada period from June-February (Bernardo & Plotkin, 2007; Ramirez Acevedo, Martinez Blas, & Fuentes-Mascorro, 2012). Although many beaches worldwide along 32 different countries are suited for solitary nesting (Spotila, 2004), only a few are suited for arribada nesting, located in Costa Rica (Ostional and Nancite), India (Gahirmatha) and Mexico (La Escobilla) (Bernardo & Plotkin, 2007; Spotila, 2004). The world main arribada beach is located in the marine protected area of "La Escobilla", on the Pacific side in Oaxaca, Mexico (Valverde et al., 2012). Despite being the most abundant species of sea turtle, olive ridleys have undergone a 30-50% reduction in their historical global population size. There is only one major nesting site left in Mexico, La Escobilla, and two minor ones, Ixtapilla and Morro Ayuta (Albavera Padilla, 2007). As consequence, the Mexican population is classified as endangered (Abreu-Grobois & Plotkin, 2008).

Olive ridley are active pelagic predators, hunting on 77% of their dive durations, and can occupy different habitats according to their population (Chambault et al., 2016; McMahon et al., 2007). Foraging grounds have been associated with the high presence of micronekton biomass and their carnivorous generalist diet includes crustaceans, cephalopods, fishes and jellyfishes (Chambault et al., 2016). This large foraging area makes them more susceptible to fisheries by-catch. Despite being the smallest sea

turtle, olive ridleys exhibit long duration, deep dives when foraging pelagically. Mean

dive duration for a large sample of adult females was 46 min. Dives as long as 200 min

(3.3 hours) and as deep as 300 m have been reported (Chambault et al., 2016;

McMahon et al., 2007; Polovina, Howell, & Balazs, 2003; Stabenau & Heming, 1994).

Our primary objectives were to 1) measure plasma and blood volume and

estimate tissue oxygen stores in large sample of free- ranging adult female olive ridley

sea turtles during nesting; 2) compare blood oxygen stores and associated variables

between the arribada and solitary nesting periods; 3) estimate cADL for the sampled

olive ridley sea turtles at a range of water temperatures and activity levels and compare

these estimates to published diving behavior. As a mostly pelagic and highly migratory

species, we hypothesize that newly arrived turtles, nesting in arribadas, will exhibit an

increased cADL as compared to solitary nesting towards the end of the season, where

turtles have likely become neritic.

METHODS

Field site and sampling

All animal handling procedures were approved by the Sonoma State University

IACUC and performed under collecting permit SGPA/DGVS/12915/16. Samples were

exported for laboratory analysis to Sonoma State University under exporting/importing

permits CITES MX88143 and CITES 19US85728C/9. Nesting olive ridley females were

sampled at the marine protected area of La Escobilla, Oaxaca, Mexico (15º 47' N; 96º 44'

W; Figure 1) during solitary nesting in February 2017 (n = 10) and during the arribada in

November, 2017 (n = 13). Handling and sampling were performed while the turtle was nesting, after digging the nest, since this is when females enter a 'trance-nesting period' (Dutton, 1996); and we were less likely to disrupt nesting. None of the females were disturbed from their nesting, nor returned to the sea without laying their eggs.

Females sampled during solitary nesting were weighed using a hand-held scale (± 0.1 kg). Because of an equipment failure it was not possible to weigh the females sampled during arribada nesting. For these females, mass was estimated using a regression from published data on olive ridley morphometrics (Espinoza-Romo et al., 2018; n= 59, mass = -47.44 + 1.13 x SCL, r^2 = 0.70, p < 0.001.). This equation predicted the mass of the turtles that were weighed with a mean error of 4%.

All blood samples were collected from the cervical vein (Dutton, 1996; Mettee, 2014). An initial blood sample was taken into a heparin Vacutainer tube to measure hematocrit and hemoglobin values. Females were injected with Evan's Blue dye (~ 1 mg/kg) and plasma volume was calculated after corrected for hemolysis (El-Sayed, Goodall, & Hainsworth, 1995). Three sub sequential blood samples were taken at approximately 7-minute post injection intervals. Syringes were calibrated gravimetrically to determine precise injection volume. Blood samples were kept on ice for 20 minutes until centrifuged at the field site. All plasma samples were frozen after centrifugation at -20^0C until laboratory analysis.

Blood oxygen stores

Hemoglobin (Hb) concentration, hematocrit (Hct), plasma volume (V_p) and mean corpuscular hemoglobin concentration (MCHC) were determined for each animal.

Hematocrit was calculated by standard microcentrifugation, averaging three values for each sample. Absorbance of Evans Blue dye in the plasma was determined at 624 and 740 nm. Values at 740 nm, which do not absorb blue, were used to calculate the blank optical density at 624 nm and correct for hemolysis and precipitate (Foldager & Blomqvist, 1991). Values from serially collected Evans Blue samples were log-transformed, fit to a regression line, and the *y*-intercept was used to determine the instantaneous dilution volume by comparing to a serial dilution of the injectate (El-Sayed et al., 1995). Blood volume (V_B) was calculated as V_P (1 − Hct/100), where V_P is absolute plasma volume. Hb concentration was measured using the cyanmethemoglobin method (Sigma D5941, St. Louis, MO). Mean corpuscular Hb concentration (MCHC) was calculated as 100 Hb Hct^{-1}. Total available blood oxygen stores were calculated assuming one-third of blood was arterial and two-thirds of blood was venous (Lutz & Bentley, 1985), 95% and 80% saturation, respectively (Lutcavage, Bushnell, & Jones, 1990) and a Hb oxygen carrying capacity of 1.34 ml O_2 g^{-1}.

Total O_2 stores and cADL

Muscle O_2 stores were estimated assuming 22% of mass is muscle (Lutz & Bentley, 1985) and a Myoglobin (Mb) concentration of 3.1 mg g^{-1} muscle tissue. Lung O_2 stores were estimated using an allometric equation for lung volume (Hochscheid et al., 2007) and assuming the inspired air was 17.4% O_2 (Berkson, 1966). Oxygen consumption rate was estimated using the equation developed for captive loggerhead turtles that incorporates water temperatures and activity levels (Williams et al., 2019). Finally, cADL was calculated as the total body oxygen stores divided by the oxygen consumption rate.

We calculated cADL for each individual turtle at 100% activity and a mean water temperature of 26°C, the average temperature recorded for free-ranging olive ridleys (Chambault et al., 2016). We visualized cADL for total O_2 stores and for the contribution of blood O_2 stores across a range of activities from 0-100% and water temperatures ranging from 18.7°C to 30°C, the range of water temperatures encountered by free-ranging olive ridleys (Chambault et al., 2016; McMahon et al., 2007).

Statistical analysis

Statistical analysis was performed using JMP Pro 14 (SAS Institute, USA). Variables of interest were compared between the arribada and solitary nesting samples using two-sample t-tests with pooled or unequal variance. Unequal variance was assessed using Levene's test. Relationships to body mass were assessed using simple linear regression. Statistical significance was considered at p=0.05.

RESULTS

Blood oxygen stores

Values for olive ridleys' mass (M_b kg), Hb (g dL^{-1}), Hct (%), MCHC (g dL^{-1}), V_P (mL kg^{-1}) and V_B (mL kg^{-1}) on wild nesting solitary females (n=10), wild nesting arribada females (n=13) and their averages are presented in Table 1. Blood Hb did not vary between nesting periods (p = 0.14) but was more variable during the arribada period (Levene's test, p = 0.03). Hct was similar during the 2 nesting periods (p = 0.38). The variation in Hb content was unrelated to Hct (p = 0.33), due to individual differences in

calculated MCHC. MCHC did not vary between nesting periods (p = 0.58) but was more

variable during the arribada period (Levene's test, p = 0.03).

Mean V_P increased significantly with increased body mass (V_P = 28.3*mass +

795.4, r^2=0.31, $F_{1,21}$=9.37 p<0.006; Figure 2). V_P was 5.4 ± 0.4 (SD) % of body mass and

this percentage was greater during the arribada period (t = 3.04, df = 21 p = 0.006). V_B,

calculated using V_P and Hct was not related to body mass (p = 0.35; Figure 3). V_B was 8.1

± 1.3 (SD) % of body mass and this percentage did not vary between nesting periods (p =

0.17). Estimated mass specific blood O_2 stores were 7.74 ± 1.8 (SD) ml O_2 kg^{-1}. This value

did not vary between nesting periods (p = 0.92), but was more variable during the

arribada period (Levene's test, p = 0.008; Figure 4).

cADL and diving behavior

cADL (min) from estimated total O_2 stores was calculated for water

temperatures ranging from 18.7°C – 30.0°C (Chambault et al., 2016; McMahon et al.,

2007) and for activity levels of 0-100% of the dive (Kinoshita, Fukuoka, Niizuma,

Narazaki, & Sato, 2018; Williams et al., 2019) (Figure 5A). At 26°C, the mean

temperature value encountered by olive ridley's during their post-nesting migration

(Chambault et al., 2016), cADL ranged from 40.5 ± 2.8 min to 85.8 ± 5.9 min depending

on activity levels. Blood oxygen stores represented 32.2 ± 5.2% of estimated total body

oxygen stores. Thus, blood O_2 stores added 13.52 ± 2.9 to 27.9 ± 6.2 min to aerobic dive

times in 26°C water. In the coldest water (18.7°C) and at rest (0% activity), blood O_2

stores added 42.7 ± 9.4 min to aerobic dive times (Figure 5B).

DISCUSSION

For a large sample of free-ranging nesting olive ridley sea turtles, blood volume was 7.6 ml kg^{-1} body mass and blood O_2 stores were 7.2 ml O_2 kg^{-1}. This represents ~32% of body oxygen stores when making standard assumptions on lung volume and muscle stores. These stores may represent a critical component of aerobic capacity on the longest and deepest dives exhibited by individuals of the species. Mass specific blood volume was similar to that reported for leatherbacks (7.7%; Table 2) and was slightly higher than that reported previously for other chelonidae (6.6-6.7%; Thorson, 1968). However, as previously reported, blood volumes were not remarkable when compared to terrestrial species (Thorson, 1968).

Mass specific blood volume and blood oxygen stores varied widely among individuals, 2-fold and 3-fold, respectively. Plasma volume was relatively invariant and most of these differences were due to variation in hematocrit, Hb and associated MCHC content. This wide individual variation in blood oxygen stores emphasizes the importance of physiological state to aerobic capacity and the value of having a large sample size for assessing capacity of a species. Hb concentrations decreased weakly with body mass, but the drivers of widely varying hematocrit and most of the variation in Hb content of blood is unknown. Large sample size studies of sea turtle hematology yield similarly wide ranges of Hct among individuals (e.g. (Lewbart et al., 2014; Rousselet et al., 2013; F. E. Wood & Ebanks, 1984) and have demonstrated associations of Hct with stress, contaminant burdens, ectoparasites and tumor scores (García-Párraga et al., 2014; Keller, Kucklick, Stamper, Harms, & McClellan-Green, 2004; Stamper et al., 2005;

Work & Balazs, 1999). A significant correlation between Hct and the straight carapace length of sea turtles has been previously reported (F. E. Wood & Ebanks, 1984) but we found no relationship to mass or size in our study.

We compiled published body mass, Hct, Hb content, BV and MCHC values for five species of sea turtles (Table 2). When compared to the other species, olive ridley sea turtle has the lowest Hct and Hb values. MCHC values were relatively consistent among other species, with the exception of the deep-diving *D. coriacea*. However, *Lepidochelys kempii and L. olivacea* are closely related to each other (Crawford et al., 2015) and as such, MCHC values are very close to each other. Given this relationship, it would be expected that both species will be well adapted to increase their diving time by the use of total blood oxygen stores. But this is not the case, as *L. kempii* has not been documented to exhibit such deep dives like *L. olivacea*. In fact, *L. kempii* exhibit the shallowest dives of all sea turtles, with the deepest recorded dive of 5.3 m (Williard, 2013). *D. coriacea* is the species that had the largest values of mass-specific blood volume, but this was expected since they are the deepest divers from all seven species (Robinson & Paladino, 2015). What was most surprising was the striking similarity on V_B values between *D. coriacea* (7.7 ml kg^{-1}) *and L. olivacea* (7.6 ml kg^{-1}) sea turtles. This supports previous observations of *L. olivacea* as being the second-deepest diver (300 m; Stabenau & Heming, 1994) of all species of sea turtles after *D. coriacea* (1280 m; López-Mendilaharsu, Rocha, Domingo, Wallace, & Miller, 2008). Blood O_2 stores may be especially critical if pulmonary shunts are activated as part of the dive response to avoid decompression injuries on the deepest and longest dives (García-Párraga et al., 2018).

Interestingly, olive ridley sea turtles newly calculated blood O_2 stores are similar to those reported for the best avian divers, emperor penguins (*Aptenodytes forsteri*) (Ponganis et al., 2011), with blood stores representing 31% of body O_2 stores.

We found no significant difference in blood O_2 stores or associated variables between the two nesting periods. A previous study found that Hct is higher in migrating turtles compared to nesting values (Yang et al., 2019). This difference was thought to be due to conditioning effects from longer, deeper dives during the migratory phase. We found no similar evidence of conditioning between recently arrived arribada turtles and turtles that had spent several months in residence during internesting intervals. One possible explanation for this finding is that our sampled turtles are residents of La Escobilla—as it has been demonstrated that olive ridley populations differ widely in habitat use (Chambault et al., 2016; Polovina et al., 2004).

Although there were no significant differences between nesting periods, several measured variables were more variable during the arribada nesting. Females were heavier during arribada. Hct, Hb, MCHC and mass-specific blood O_2 stores are all more variable during the arribada nesting. The underlying cause of this variability was not due to differences in mass and likely reflects physiological state. These differences may reflect differences in habitat use among the arriving turtles (i.e. migratory or resident). A recent study on transport stress in Kemp's ridley showed that the stress of transport increased variability in Hct in association with changes in corticosterone and glucose concentrations (Hunt et al., 2019). A study on different stress-responses between solitary and nesting females found that arribada nesting turtles exhibited slower

elevation of corticosterone in response to a stress test but did not compare baseline levels (Valverde, Owens, Mackenzie, & Amoss, 1999). Future studies should evaluate potential modulators of the increased individual variation seen during this nesting period.

Based on measures of diving behavior in olive ridley sea turtles, blood O_2 stores are likely a critical component of aerobic respiration to many dives. Lung stores are similar among species, suggesting that diving differences might be most likely due to individual variation in blood O_2 stores rather than in muscle stores, given low myoglobin constants across species; ~4% of total body O_2 stores (Berkson, 1966; Lutz & Bentley, 1985; Stabenau & Heming, 1994). Previous investigations reporting deep and long dive behaviors exhibited by olive ridley sea turtles (Chambault et al., 2016; McMahon et al., 2007; Polovina et al., 2004) demonstrated that 77% of dive time represents active foraging behaviors, and that some dives exceed the presumed depths of lung collapse (~120 m, Berkson, 1967). Our cADL estimates that incorporate blood stores of ~41 min for dives with high levels of activity and at mean water temperatures as reported for foraging dives, suggesting that blood O_2 stores provide ~14 min of dive time and are necessary to support the diving behavior on the majority of dives. Recorded average dive duration in olive ridleys is ~46 min (Chambault et al., 2016). All dives are likely aerobic as their short and invariant post-dive surface times do not suggest that turtles are incurring a lactate debt and use of pulmonary shunts to avoid decompression injury on some deep dives may further emphasize the importance of blood stores (García-Párraga et al., 2018).

Conservation Implications

Bycatch, the primary mortality threat to sea turtles, often results in death from drowning or signs of decompression sickness in 43% of incidental captures (García-Párraga et al., 2014). The evidence for decompression injuries in incidentally captured turtles, emphasize the importance of modulation of lung perfusion during diving in sea turtles and the potential for loss of access to lung stores during all or parts of dives. Individual and interspecific variation in blood O_2 stores may be an important factor in avoiding drowning when captured in fishing nets.

The primary determinant of rates of oxygen use in diving sea turtles is activity levels (Williams et al., 2019). However, given high rates of activity on most foraging dives, water temperature is also an important modulator of diving metabolism. Changes in water temperature due to global warming can directly affect ectothermic body temperature and lower breath-hold capacity. Based on our calculations a 1 degree change in mean water temperature reduces aerobic dive time by ~6% at high activity levels. Further, changes in thermal structure, currents and prey distribution in response to climate change may require substantial alterations to diving behavior (Hawkes et al., 2009; Poloczanska, Limpus, & Hays, 2010). Individual and interspecific variation in blood O_2 stores may be a crucial component of enabling behavioral plasticity in response to these changes.

CONCLUSION

The first large sample study on blood O_2 stores in olive ridley sea turtles revealed that these stores represent a critical component of total body O_2 stores. Mass-specific

blood volumes were similar to that reported for larger deeper diving leatherback sea

turtles and appear to be essential to support the long duration diving behavior reported

for olive ridleys. The wide individual variation in blood O_2 stores has important

implications for intraspecific variation in breath-hold ability. This variation was greater

during the arribada nesting period due to increased variation in both hematocrit and

MCHC. High blood O_2 stores may be a critical component of the behavioral plasticity

needed to respond to changes in prey distribution, thermal structure and currents that

result from climate change.

Appendices

Table 1. Values from arribada nesting, solitary nesting and their averages. Values presented are least square means ± standard error mean. M_b = body mass; Hb = hemoglobin; Hct = hematocrit; MCHC = mean corpuscular hemoglobin concentration; PV = plasma volume; BV = blood volume. * denotes significant differences between the nesting periods ($p < 0.05$).
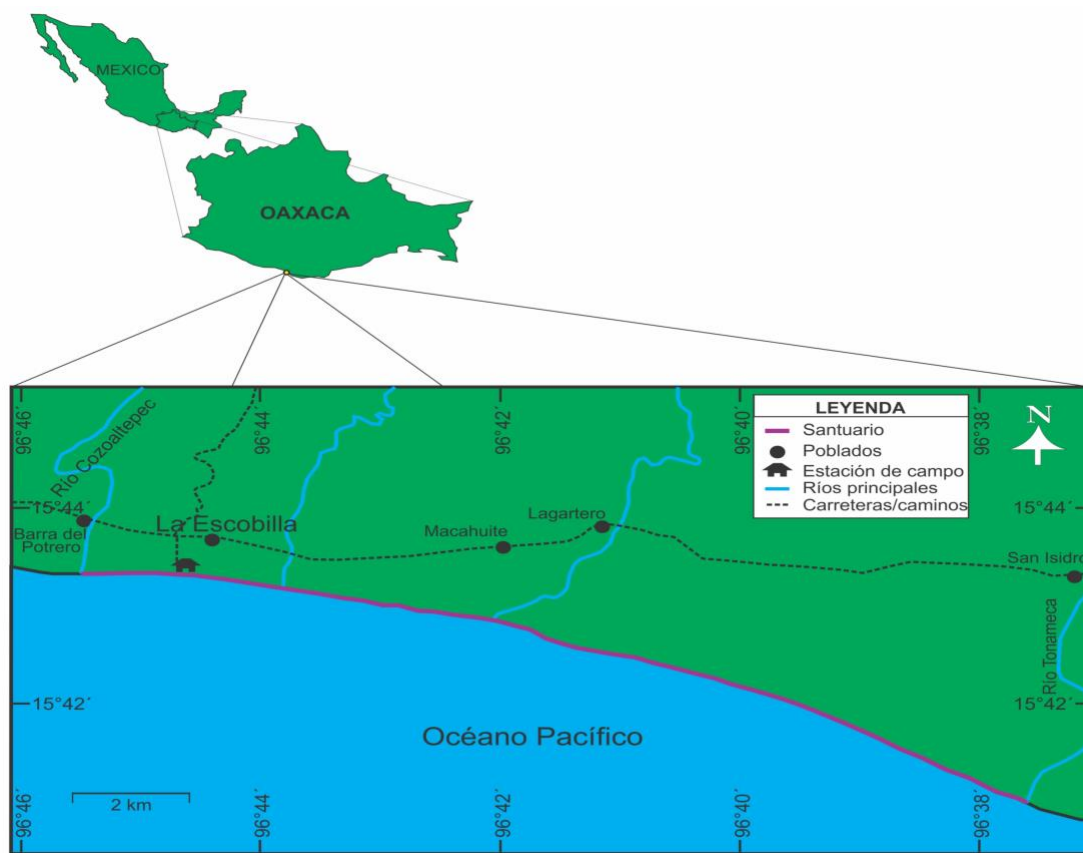
	Arribada Nesting	Solitary Nesting	Average	Range
M_b (kg)	34.9 ± 1.3*	29.6 ± 0.9	32.6 ± 1.0	22.3 - 40
Hb (g dL $^{-1}$)	8.9 ± 0.5	9.7 ± 0.2	9.2 ± 0.3	6.0 - 12.9
Hct (%)	30.6 ± 2.4	32.9 ± 0.8	31.6 ± 1.4	18 - 50
MCHC (g dL $^{-1}$)	0.31 ± 0.03	0.30 ± 0.01	0.31 ± 0.01	0.18 - 0.43
PV (mL)	1768.1 ± 44.8*	1506.5 ± 43.6	1654.4 ± 41.5	
PV (mL kg $^{-1}$)	5.1 ± 0.1	5.1 ± 0.1	5.1 ± 0.4	4.4 - 6.1
BV (mL)	2593.3 ± 121.8*	2247.9 ± 68.7	2443.1 ± 82.12	
BV (mL kg $^{-1}$)	8.4 ± 0.1	7.6 ± 0.1	8.1 ± 0.1	5.8 - 11.4
Blood O$_2$ (mL kg^{-1})	7.8 ± 0.6	7.8 ± 0.3	7.8 ± 0.4	3.6 – 10.8

Table 2. Mean blood values for *L.* olivacea from this study and other species of sea turtles. Hb values are expressed as (g/100 mL blood).

Common Name	Body Mass (kg)	Hct (%)	Hb (g dL^{-1})	MCHC (Hb/Hct)	Blood volume (ml kg^{-1})	Reference
Olive ridley	31	32	9.2	0.29	7.8	This study
Kemp's ridley	37.8	32	10.1	0.30	6.7	1,2,3
Loggerhead	35	41	9.8	0.24	6.7	1,4
Hawksbill	24	39	9.6	0.24	-	5
Green turtle	145	45	10.6	0.23	6.6	6,7
Leatherback	300	39	15.6	0.40	7.7	8,9

[1] Thorson, 1968, [2] Davis, 1991, [3] Marquez-M, 1994, [4] Keller et al., 2004, [5] Muñoz-Pérez et al. 2017, [6] S. C. Wood et al., 1984, [7] F. E. Wood & Ebanks, 1984, [8] Lutcavage, Bushnell, & Jones, 1990, [9] Lutcavage, Bushnell, & Jones, 1992.

Figure 2. Marine Protected Area La Escobilla. Field site located in the Pacific Ocean in Oaxaca, Mexico. Figure by E. Albavera.

Figure 2. Plasma volume increased with body mass. Open circles denote arribada nesting and closed circles denote solitary nesting (r^2=0.68, p<0.0001). Plasma volume was calculated from dilution of Evan's Blue dye.
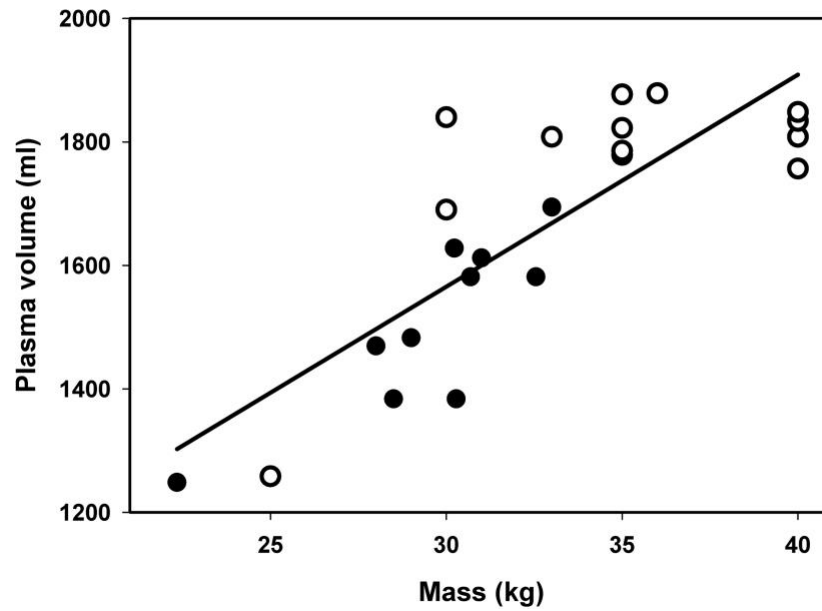
Figure 3. Blood volume increased weakly with body mass. Open circles denote arribada nesting and closed circles denote solitary nesting (r^2=0.16, p=0.06). Blood volume was calculated as PV [(100 − Hct)$^{-1}$].
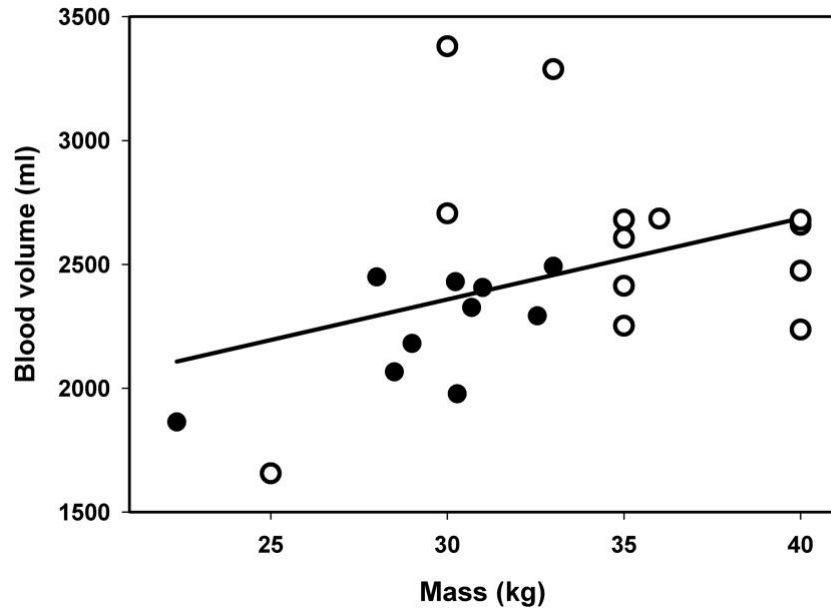
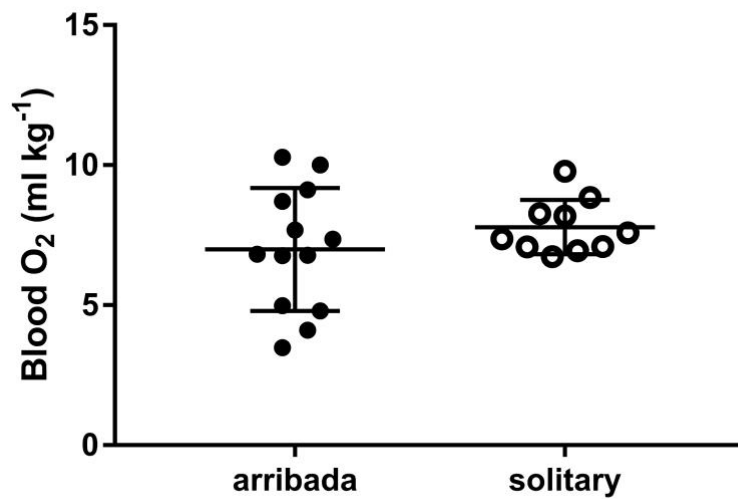**Figure 4**. Mass specific blood oxygen stores calculated from plasma volume and Hct. Stores were more variable during the arribada nesting period (Levene's test, p = 0.04).

Figure 5. Estimated cADL from total O_2 stores (A) and blood O_2 stores (B) at water temperatures ranging from 21.5°C - 30.0°C and 0-100% activity during the dive. Diving metabolic rate was estimated using Equation 1 from Williams et al., 2019.
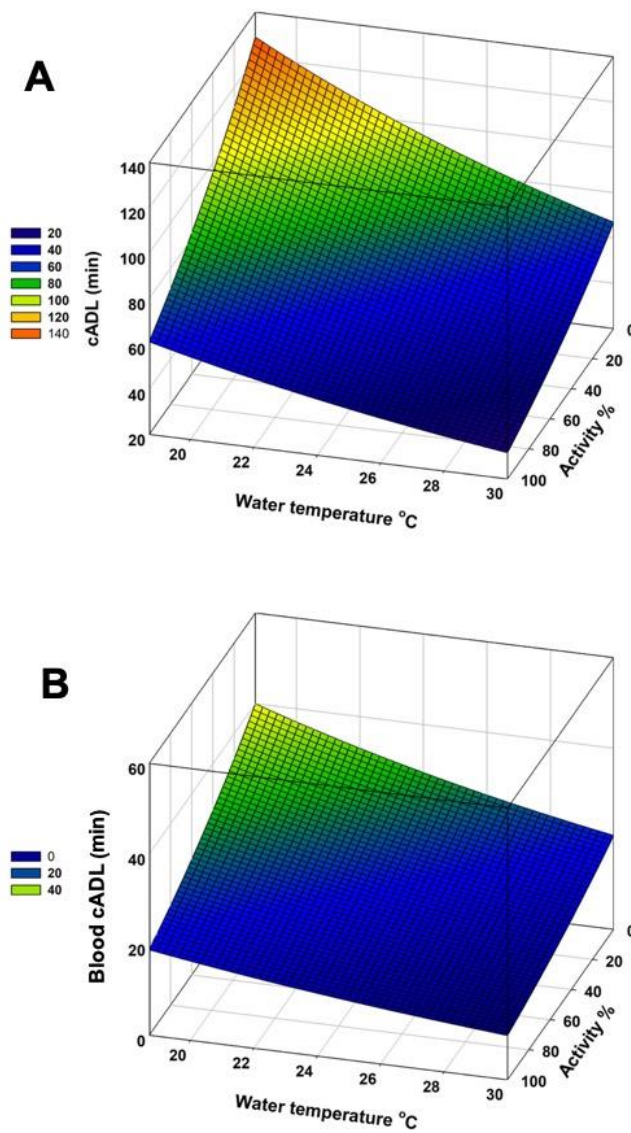
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