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In situ swimming behaviors and oxygen consumption rates of juvenile lemon sharks (*Negaprion brevirostris*)

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Abstract Knowing how often animals engage in different behaviors and their energetic costs may explain why animals behave the way they do in the wild. This study sought to investigate the relationship between the frequency of various swimming behaviors and their associated energetic costs (oxygen consumption rates) in situ for juvenile lemon sharks (*Negaprion brevirostris*). Behaviors were identified for captive animals and remotely observed for animals in the wild with accelerometers, and oxygen consumption rates of behaviors were estimated using acceleration-calibrated relationships. Lemon sharks rested infrequently (4.3% of deployment), and the occurrence of active swimming behaviors was inversely related to their respective oxygen consumption rates. Furthermore, time of day and tide state influenced when lemon sharks exhibited active swimming behaviors – but not resting – such that sharks were most active during the day on flooding tides. Oxygen consumption rates also differed across and within different behaviors with time of day and tide state, although mean oxygen consumption rates were highest on daytime flooding tides and uniformly reduced across all other diel and tide combinations. Despite variation in oxygen consumption rates, however, lemon shark activity occurred at 32.3–35.6% of their aerobic metabolic scope. These data do not provide a clear oxygen consumption basis for swimming behaviors observed in situ, which may have been masked by potentially stronger ecological drivers (e.g., predator-prey dynamics). However, these data are relevant to linking behavioral modifications to changes in energy use that shows much promise for addressing conservation issues in fishes.

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Introduction

Swimming is an inherently costly, yet important activity among fishes. Swimming facilitates energy acquisition to survive and reproduce, the rate of which is linked to population growth (Lemon 1991). In other words, a swimming fish must acquire energy at a faster rate than it uses energy, and swimming is an energetically costly activity (Boisclair and Leggett 1989; Boisclair and Sirois 1993). For some species,

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swimming behaviors comprise the largest and most variable component of a fish's energy budget (Boisclair and Sirois 1993; Lowe 2001). Indeed, fishes can devote the majority of their aerobic metabolic scope to sustaining routine activity (Lowe 2001; Dowd et al. 2006; Murchie et al. 2011). Furthermore, variation in energy expenditure tied to swimming behaviors alone can considerably affect growth rates and, ultimately, fitness (Rennie et al. 2005; Cooke et al. 2016). Energy expenditure generally increases exponentially with increases in swimming velocity (e.g., cruising, migrating), and the recruitment of anaerobic metabolism for brief, intermittent, and intense behaviors (e.g., burst swimming, mating) can considerably increase rates of energy expenditure (Brett 1964).

Linking energy expenditure to discrete behaviors is key to understanding why fish behave the way they do in the wild. However, the link between energy use and behavior can be quite vague, and just what constitutes a "discrete" and measurable behavior requires clear definition (e.g., kinematic thresholds, metabolic pathways). Indeed, studies addressing the energetic costs of ecologically important behaviors, such as those related to predator-prey interactions or reproduction, would be of great value to better understanding a species' ecology, developing robust bioenergetics models, and addressing conservation issues (Cooke et al. 2016; Treberg et al. 2016). Furthermore, assigning energetic costs to simple behaviors, such as those related to swimming activity can be quite informative. For instance, Barnett et al. (2016) demonstrated that provisioning whitetip reef sharks (*Triaenodon obesus*) at ecotourism sites led sharks to rest less during the day and, therefore, expend more energy. Furthermore, Clark et al. (2012) determined the energetic cost for exhaustive activity associated with fisheries capture for Coho salmon (*Oncorhynchus kisutch*). Thus, understanding how much energy fishes devote to various behaviors in the wild has much to offer to basic and applied animal ecology.

Deploying electronic telemetry packages on animals in their natural habitat can provide critical data on their behavior and energy use. The application of accelerometry to biotelemetry and biologging studies has made it possible to remotely observe behaviors of fishes in the wild (Brownscombe et al. 2014; Wilson et al. 2015), and estimate activity-specific energy use (Wilson et al. 2013; Brownscombe et al. 2017). Specifically, acceleration biologgers record high-resolution

data in one or more axes, thereby making it possible to distinguish behaviors based on the frequency and amplitude of acceleration signals and device orientation (Shepard et al. 2008; Sakamoto et al. 2009). In addition, validation studies have determined that acceleration-based behavioral metrics are reliable proxies of energy use for teleost and elasmobranch fishes (Gleiss et al. 2010; Wright et al. 2014). Acceleration biologgers, therefore, are powerful tools for remotely monitoring behavior and estimating rates of energy expenditure for fishes in situ (Brown et al. 2013; Metcalfe et al. 2016). While these approaches have been implemented for laboratory and mesocosm studies (Whitney et al. 2007; Gleiss et al. 2010; Bouyoucos et al. 2017b), few studies have applied these accelerometry techniques to fishes in the wild (Murchie et al. 2011; Wilson et al. 2013; Brownscombe et al. 2017).

The primary objective of this study was to quantify the relationship between activity-specific oxygen consumption rates in relation to swimming behaviors in situ for a fish. We predicted that the occurrence of swimming behaviors would be negatively related to oxygen consumption rates, with swimming behaviors being increasingly rare as oxygen consumption rates increase. To accomplish this, we conducted a series of laboratory and field experiments to assign accelerometric characteristics to swimming behaviors for remote observation, and to estimate the occurrence of swimming behaviors and their oxygen consumption rates for fish in the wild. Together, these objectives may present a potential physiological explanation for the occurrence of swimming behaviors in a fish.

Materials and methods

Animal collection and husbandry

Juvenile lemon sharks (*Negaprion brevirostris*) were collected from tidal mangrove creeks around Cape Eleuthera, Eleuthera, The Bahamas (24°49′46.43" N, 76°19′41.49" W) using block seine netting (Bouyoucos et al. 2017b). Juvenile lemon sharks were targeted for this study because of their abundance, strong site fidelity, and lack of seasonal habitat use (Murchie et al. 2010; Harborne et al. 2016), which facilitates retrieval of biologging devices from free-swimming animals (Metcalfe et al. 2016). In addition, accelerometry and respirometry techniques, which are necessary for remote

behavioral telemetry and estimating field oxygen consumption rates of sharks in the wild, have been successfully applied to lemon sharks (Bouyoucos et al. 2017b; Lear et al. 2017).

A subset of sharks were transported by boat in 200 L coolers to a wet lab facility for observation to assign accelerometric characteristics to swimming behaviors. These sharks were held in 13,000 L (3.7 m diameter by 1.25 m deep) flow-through holding tanks and fed a daily ration (6.0% of body mass per day) of commercially available frozen Spanish sardines (*Sardinella aurita*) to satiation. Sharks were maintained in captivity for no more than four weeks, and were released to their capture site following experimentation.

Acceleration biologgers

Externally-attached tri-axial acceleration biologgers (hereafter, accelerometers) were used throughout each component of this study. Accelerometers (X16-mini, Gulf Coast Data Concepts, Waveland, MS, USA; 5.1 cm × 2.5 cm × 1.3 cm, 4.6 g in water; 25 Hz recording frequency; ± 16 g acceleration range, 1 g = 9.8 m s^{-2}) were prepared and attached uniformly, in under two minutes, on the right side of the first dorsal fin, following standardized methods for X16-mini accelerometers (Bouyoucos et al. 2017b). It should be noted, however, that the X16-mini accelerometer configuration affects the swimming kinematics, activity levels, and swimming performance of small (70.4 ± 6.6 cm total length) lemon sharks (Bouyoucos et al. 2017a). Prior to deployment, accelerometers were rotated 360 degrees through all three axes to calibrate device output against gravitational acceleration (Sakamoto et al. 2009; Gleiss et al. 2010).

Acceleration ethogram

Accelerometer-equipped sharks were observed swimming in an enclosed natural habitat to relate known behaviors with acceleration data and generate an acceleration ethogram. Five lemon sharks (70.8 ± 3.5 cm total length, 1.8 ± 0.2 kg; mean ± S.D.) were outfitted with individually color-coded accelerometers and released into a 4000 m^2 saltwater pond mesocosm (Bouyoucos et al. 2017b) immediately adjacent to the wet lab holding facility. Sharks were released to the mesocosm as a group because juvenile lemon sharks are known to be gregarious, although it is unknown to what extent individual tendencies to assort with conspecifics based on behavior and activity levels affected generation of the acceleration ethogram (Wilson et al. 2015). Following 24 h of acclimation, sharks were haphazardly selected for observation by an observer with a digital watch that was synchronized with the accelerometers. The start and stop times were recorded for four swimming behaviors (Gleiss et al. 2009): "resting" (remaining stationary on the substrate and buccal pumping), "swimming" (swimming supported by a continuous and consistent tailbeat), "fast swimming" (swimming supported by a fast, unsteady tailbeat), and "burst swimming" (one or more rapid tailbeats proceeded by a short-lived increase in speed). Sharks were observed between 07:00–08:00, 11:00–12:00, and 15:00–16:00 over three days. Observation did not occur past 16:00 because of diminishing light levels. Previous observational studies in the mesocosm have documented variable and contrasting diel activity patterns in juvenile lemon sharks, and it was, therefore, assumed that daytime observation would sufficiently characterize the range of activity levels associated with each swimming behavior (Wilson et al. 2015; Bouyoucos et al. 2017b). Water temperature was recorded from a fixed site at the mesocosm during each observation with a field dissolved oxygen and conductivity meter (YSI Pro2030, YSI Incorporated, Yellow Springs, OH, USA).

Field deployments

Accelerometers were deployed on a second group of juvenile lemon sharks to generate acceleration data to estimate the frequency of swimming behaviors and energy expenditure of lemon sharks in situ. Ten juvenile sharks (70.2 ± 3.8 cm total length) were collected from Kemps Creek, which is a high-use tidal mangrove creek for lemon sharks (Murchie et al. 2010) and movement in and out of the creek is restricted to a single opening that can be blocked off with a seine net. Accelerometers were attached in under two minutes in the same manner described above. Attempts to recapture sharks were made within a week of deployment. When sharks were recaptured, accelerometers were quickly removed by cutting the line at the backing plate opposite the

accelerometer, and sharks were released back to their capture site. Water temperatures during deployments were 29.6 ± 0.2 °C.

Data analysis

Acceleration ethogram

Acceleration data generated during mesocosm observations were categorized into one of four swimming behaviors (resting, swimming, fast swimming, and burst swimming) to generate a classification tree (De'ath and Fabricius 2000; Nathan et al. 2012) that was used to assign swimming behaviors to acceleration data generated by field deployed sharks (Bouyoucos et al. 2017c). First, acceleration data for one instance of each behavior per time of day per shark were partitioned into dynamic (shark) and static (gravity) components with a two-second smoothing interval (Bouyoucos et al. 2017b, 2017c). Next, eleven acceleration metrics were calculated using Igor Pro (6.3.3.5, WaveMetrics, Inc., Lake Oswego, OR, USA) to generate a classification tree with the "tree" package in R (R Core Team 2015; Ripley 2016): means and standard deviations of raw acceleration data in each axis over one-second intervals (Brown et al. 2013), overall dynamic body acceleration (ODBA; Wilson et al. 2006), pitch and roll angles (Brownscombe et al. 2014), tailbeat frequency (TBF; Kawabe et al. 2003) and tailbeat acceleration amplitude (TBAA; Sakamoto et al. 2009).

Field deployments

Acceleration data generated during field deployments were analyzed to determine the frequency of occurrence of swimming behaviors and their associated aerobic costs. The beginning of each deployment was analyzed to determine when sharks resumed consistent activity levels, indicating recovery from handling. Specifically, ODBA was averaged every minute and binned into ten-minute bins, the means of which were compared with an ANOVA for the first 120 min of deployment. Multiple comparisons with Tukey's Highly Significant Difference test were conducted to identify the time when the value of one bin was not significantly different from the chronological next bin (Bullock et al. 2015). Acceleration data from before sharks recovered from handling, and after

seine nets were set to recapture sharks were excluded from further analysis. The same 11 metrics used to generate the classification tree were calculated for every second of deployment for each shark, and were run through the classification tree model to assign a behavior to each second of acceleration data.

Instantaneous oxygen consumption rates ($\dot{M}O_2$) were used to determine field $\dot{M}O_2$ ($\dot{M}O_{2Field}$) and the mean $\dot{M}O_2$ of swimming and fast swimming behaviors. Instantaneous $\dot{M}O_2$ for swimming and fast swimming behaviors were estimated using the equation $\dot{M}O_2 = 136.5 + 92.8\text{TBF}$ generated from juvenile lemon sharks at Cape Eleuthera and at 30.0 °C (Bouyoucos et al. 2017b). Burst swimming $\dot{M}O_2$ was not estimated because burst swimming utilizes anaerobic metabolism, the costs of which cannot be accounted for by our calibration equation. Maximum $\dot{M}O_2$ ($\dot{M}O_{2Max} = 398.0$ mg O_2 kg^{-1} h^{-1}) was used as an upper limit for estimation (Bouyoucos et al. 2017b). Minimum $\dot{M}O_2$ ($\dot{M}O_{2Min} = 155.2$ mg O_2 kg^{-1} h^{-1}) was assumed to be $\dot{M}O_2$ for resting sharks (Bouyoucos et al. 2017b; Lear et al. 2017). Field $\dot{M}O_2$ was calculated as the overall mean $\dot{M}O_2$ during a deployment. Oxygen consumption rates are also presented as a percent of aerobic scope (AS = $\dot{M}O_{2Max} - \dot{M}O_{2Min}$), which was 242.8 mg O_2 kg^{-1} h^{-1} (Bouyoucos et al. 2017b). It should be noted, however, that modeling $\dot{M}O_2$ this way did not account for the effects of environmental conditions (temperature, salinity, turbidity, dissolved oxygen, pH) on $\dot{M}O_2$, or include the duration or magnitude of increases in $\dot{M}O_2$ after feeding, or any anaerobic costs, such as those incurred during predator-prey interactions or fishing capture.

Overall $\dot{M}O_2$ and proportion data for each behavior were individually fit with linear mixed effects models, with behavior category as a fixed effect and shark ID as a random effect. Additionally, $\dot{M}O_2$ and proportion data for each behavior were categorized by diel period (day or night) and tide state (flooding or ebbing) to observe temporal variability in the occurrence of swimming behaviors and their energetic costs (Bouyoucos et al. 2017b). Tide and sunrise/sunset timetables were referenced from an on-island tide recording station. For swimming and fast swimming, $\dot{M}O_2$ and proportion data were fit with linear mixed effects models with diel-tide category as a fixed effect and shark ID as a random effect. Only proportion data for resting and burst swimming were fit with a linear model, as described above. All proportion data were log-ratio

transformed because proportion data sum to 1.0 and are, therefore, not independent (Aebischer et al. 1993). The importance of fixed effects was estimated by running 1000 posterior simulations of each fixed effect. Significance was determined if the 95.0% credible interval (CI) for the distribution of fixed effect estimates did not overlap zero (Hasler et al. 2016). Linear model outputs are therefore presented as the values of the upper (97.5% CI) and lower bounds (2.5% CI) of the CI. Multiple comparisons were performed by comparing means and CIs of simulated changes in model intercepts (Hasler et al. 2016).

Results

Acceleration ethogram

The classification tree automatically categorized acceleration data as resting, swimming, fast swimming, or burst swimming behaviors using only ODBA and TBF as criteria for decision rules. The number of observations and criteria for each behavior, as well as descriptive statistics for ODBA and TBF are presented in Table 1. Acceleration data were only generated from four sharks, because one accelerometer flooded within the first day of deployment.

Field deployments

All sharks were recaptured after 39.9–130.4 h at liberty, yielding a total of 713.0 h generated from nine sharks with functional accelerometers (mean = 79.2 ± 22.8 h per shark). Activity levels (i.e., ODBA) were elevated post-release for most sharks (range = 0–70 min), but

sharks resumed consistent activity levels 25.6 ± 21.9 min post-release. Overall, sharks did not exhibit swimming behaviors in equal proportions, and swimming behaviors had different $\dot{M}O_2$ (Table 2). Juvenile lemon sharks spent the majority of each day swimming ($77.8 \pm 2.9\%$), followed by fast swimming ($17.4 \pm 2.8\%$), resting ($4.3 \pm 1.5\%$), and burst swimming ($0.4 \pm 0.2\%$; Fig. 1a). Sharks had an overall $\dot{M}O_{2\text{Field}}$ of 236.5 ± 3.5 mg O_2 kg^{-1} h^{-1} (33.5% of AS), swimming $\dot{M}O_2$ was 229.8 ± 2.6 mg O_2 kg^{-1} h^{-1} (30.7% of AS), and fast swimming $\dot{M}O_2$ was 288.7 ± 4.5 mg O_2 kg^{-1} h^{-1} (54.9% of AS) (Fig. 1b).

Lemon sharks also exhibited variation in the occurrence of behaviors at different tide states and diel periods, and $\dot{M}O_2$ of swimming and fast swimming behaviors exhibited variation over time (Table 2). Juveniles in Kemps Creek were burst swimming more often during the day ($0.6 \pm 0.3\%$) than at night ($0.2 \pm 0.1\%$) on flooding tides, and were observed burst swimming at similar frequencies on ebbing tides (day: $0.4 \pm 0.4\%$; night: $0.4 \pm 0.3\%$) (Fig. 2a). Fast swimming occurred most frequently during daytime flooding tides ($25.0 \pm 5.0\%$), followed by daytime ebbing tides ($16.2 \pm 5.5\%$), and nighttime ebbing ($12.9 \pm 4.1\%$) and flooding tides ($12.2 \pm 3.4\%$) (Fig. 2b). Sharks did not exhibit any variation in the frequency of resting behaviors (Fig. 2c). Lastly, juveniles swam less frequently during daytime flooding tides ($70.4 \pm 5.0\%$), and swam consistently across daytime ebbing ($80.9 \pm 5.5\%$), and nighttime flooding and ebbing tides ($81.7 \pm 4.2\%$) (Fig. 2d).

Overall, $\dot{M}O_{2\text{Field}}$ was highest during daytime flooding tides, and equally low across all other periods (Fig. 3a). Daytime flooding and ebbing $\dot{M}O_2$ for fast swimming did not differ, and were lower

Table 1 Values (mean ± standard error and range) for overall dynamic body acceleration (ODBA) and tailbeat frequency (TBF) used to generate a classification tree machine learning algorithm to distinguish four swimming behaviors (resting, swimming, fast swimming, and burst swimming) from acceleration data generated by juvenile lemon sharks in situ

Behavior (Observations)	Rest ($n = 9$)	Swim ($n = 12$)	Fast swim ($n = 8$)	Burst (n = 8)
Criteria	ODBA <0.03 g	TBF < 1.26 Hz ODBA ≥0.03 g	ODBA <0.31 g TBF ≥ 1.26	ODBA ≥0.32 g
ODBA (g)	0.01 ± 0.00 (0.02–0.06)	0.08 ± 0.00 (0.04–0.28)	0.15 ± 0.00 (0.05–0.50)	1.28 ± 0.18 (0.13–6.77)
TBF (Hz)	0.57 ± 0.00 (0.35–2.03)	1.09 ± 0.00 (0.51–5.28)	1.48 ± 0.02 (0.46–3.84)	4.16 ± 0.29 (0.63–8.08)

Tailbeat frequency values for resting sharks were estimated as greater than zero because spectral analysis detected periodicity in dynamic swaying acceleration signals, though TBF was coincidentally not used to distinguish resting from other behaviors

Table 2 Linear mixed effects model outputs for models explaining variation in metabolic rate and proportion of time by behavioral category, and by diel period and tide state

Response	Parameter	Mean	2.5% CI	97.5% CI
Proportion of time	Intercept	−2.96	−3.05	−2.86
	Fast swim	1.59	1.46	1.72
	Rest	0.57	0.43	0.71
	Swim	4.07	3.94	4.22
Oxygen consumption rate	Intercept	288.74	286.67	290.76
	Rest	−133.51	−136.46	−130.56
	Swim	−58.96	−61.78	−56.31
Proportion of time burst swimming	Intercept	−2.82	−2.86	−2.78
	Day × Ebbing	−0.05	−0.09	0.00
	Night × Flooding	−0.08	−0.12	−0.03
	Night × Ebbing	−0.04	−0.09	0.00
Proportion of time fast swimming	Intercept	−0.86	−1.04	−0.68
	Day × Ebbing	−0.48	−0.71	−0.25
	Night × Flooding	−0.73	−0.97	−0.48
	Night × Ebbing	−0.69	−0.94	−0.45
Proportion of time at rest	Intercept	−2.35	−2.55	−2.13
	Day × Ebbing	−0.18	−0.48	0.08
	Night × Flooding	0.18	−0.09	0.44
	Night × Ebbing	0.14	−0.12	0.41
Proportion of time swimming	Intercept	1.13	0.88	1.39
	Day × Ebbing	0.73	0.42	1.07
	Night × Flooding	0.78	0.45	1.11
	Night × Ebbing	0.77	0.45	1.11
Oxygen consumption rate	Intercept	241.74	237.96	245.39
	Day × Ebbing	−7.15	−11.49	−2.92
	Night × Flooding	−8.18	−12.51	−3.95
	Night × Ebbing	−8.09	−12.64	−3.63
Oxygen consumption rate of fast swimming	Intercept	284.70	277.70	291.52
	Day × Ebbing	−3.28	−13.09	6.35
	Night × Flooding	24.12	14.78	33.07
	Night × Ebbing	10.81	1.23	21.01
Oxygen consumption rate of swimming	Intercept	231.43	229.23	233.56
	Day × Ebbing	−3.13	−5.12	−1.26
	Night × Flooding	−2.06	−4.03	0.06
	Night × Ebbing	−2.12	−3.95	−0.28

than nighttime flooding (7.1% and 8.1% lower, respectively) and ebbing $\dot{M}O_2$ (3.3% and 4.3% lower, respectively) (Fig. 3b). Swimming $\dot{M}O_2$ was highest during flooding tides, and was comparatively lower (0.8–1.2%) during ebbing tides (Fig. 3c). Field $\dot{M}O_2$ occupied 32.3–35.6% of AS across tides and diel periods, and non-resting sharks occupied the most and least AS fast swimming during nighttime flooding tides (63.3%) and swimming during daytime ebbing tides (30.1%), respectively.
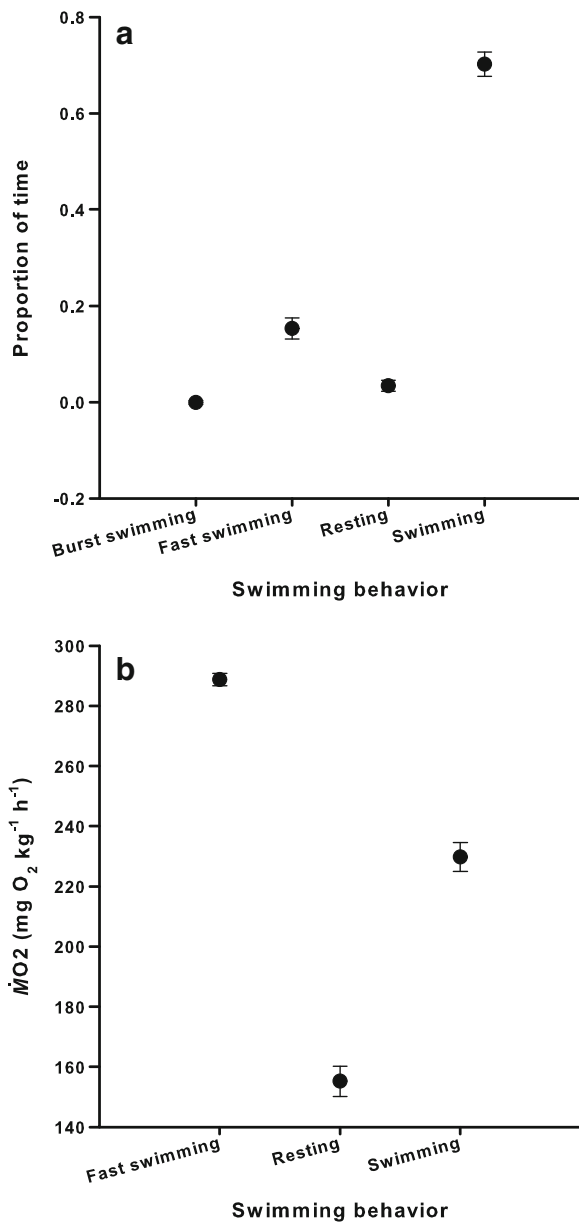
Fig. 1 Proportion of time lemon sharks exhibited four swimming behaviors, measured in situ (**a**) and their estimated oxygen consumption rates ($\dot{M}O_2$) (**b**). Data are presented as means ±95.0% credible interval. Proportion data are presented as back-transformed values because statistical analyses were performed on log-ratio transformed data to address unit-sum constraint

Discussion

Juvenile lemon sharks at Cape Eleuthera spent considerably more time swimming than resting at a cost of increased oxygen use. Specifically, juveniles at Kemps Creek were actively swimming 95.7% of the time

during deployments, and, on average, swimming and fast swimming behaviors were 148.1% and 186.0% more costly than resting. These findings contradict previous work with juvenile lemon sharks from Bimini, The Bahamas that rested 20.0–45.0% of the time (Sundström et al. 2001), or tropical whitetip reef sharks that rested at least 49.0% of the time (Whitney et al. 2007; Barnett et al. 2016). Thus, juvenile lemon sharks at Cape Eleuthera appear highly mobile for a buccal pumping species, despite the energetic savings afforded by resting relative swimming (Whitney et al. 2016). A possible physiological explanation for nearly constant activity is that lemon sharks deplete venous oxygen reserves during exercise, and may rely on ram ventilation as a more efficient mode of oxygen uptake (Bushnell et al. 1982; Steffensen 1985). Larger juveniles observed in Bimini (67–179 cm TL) might have rested more often because larger animals typically have lower mass-specific oxygen consumption rates, thereby more efficiently using oxygen for swimming (Dowd et al. 2006). Behaviorally, predator-prey interactions may drive activity levels in juvenile lemon sharks, given that juveniles have limited home range and are targets of interspecific and intraspecific predation (Murchie et al. 2010; Guttridge et al. 2012). Home range expands as lemon sharks grow larger, and larger sharks may be at less of a risk of predation, affording them increased opportunities for resting (Gruber et al. 1988; Morrissey and Gruber 1993; Guttridge et al. 2012), though juveniles at Cape Eleuthera appear to have larger home ranges than juveniles at Bimini (Murchie et al. 2010). Furthermore, hydrodynamic differences between a tidal creek (Cape Eleuthera) and a lagoon (Bimini) may differentially drive activity levels among juvenile lemon sharks (Brownscombe et al. 2017). Alternatively, it is possible that the proportion of time that sharks in this study rested was underestimated because of the influence of water current and wave action on animal-attached accelerometers (Whitney et al. 2010; Lear et al. 2017). Therefore, physiological and/or behavioral factors may drive small juvenile lemon sharks to be nearly continuously active, despite the increased energetic costs that could be avoided by resting.

Variation in the occurrence of behaviors across time of day and tide influenced overall activity costs. For sharks in this study, $\dot{M}O_{2\text{Field}}$ was highest during daytime flooding tides, when burst and fast swimming behaviors were most frequent,
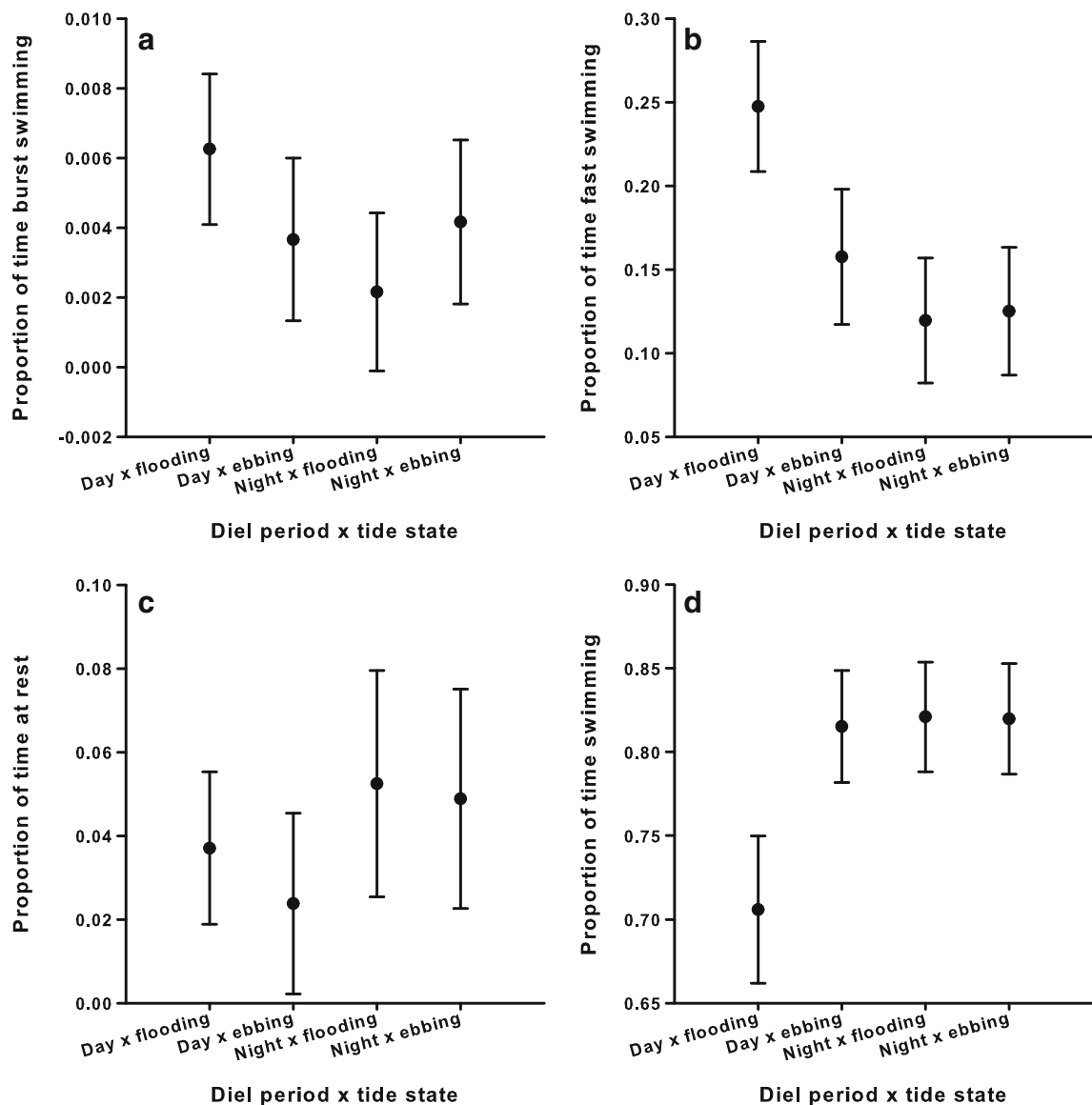
Fig. 2 Proportion of time lemon sharks exhibited burst swimming (**a**), fast swimming (**b**), resting (**c**), and swimming (**d**) behaviors, measured in situ, at day and night, and during flooding tides. Data are presented as means ±95.0% credible interval. Proportion data are presented as back-transformed values, because statistical analyses were performed on log-ratio transformed data to address unit-sum constraint

and equally low across all other time of day and tide combinations. This trend was observed even though fast swimming behaviors occurred most frequently when their associated $\dot{M}O_2$ was lowest. These results suggest that, while lemon sharks may temper how often swimming behaviors occur based on that behavior's MO_2, inherently costly behaviors will influence $\dot{M}O_{2\mathrm{Field}}$. The relatively high MO_2 associated with fast swimming behaviors likely contributed to an elevated $\dot{M}O_{2\mathrm{Field}}$, despite

the prevalence of fast swimming behaviors during daytime flooding tides. In fact, costs may have been even higher, given that fast swimming occurred within the range of activity levels that likely recruit anaerobic metabolism and precede exhaustion in juvenile lemon sharks (Graham et al. 1990; Bouyoucos et al. 2017b). Similar to our focal species, bonefish (*Albula vulpes*) also exhibit considerable variation in behavior, activity, and energy expenditure across diel and tidal periods, although
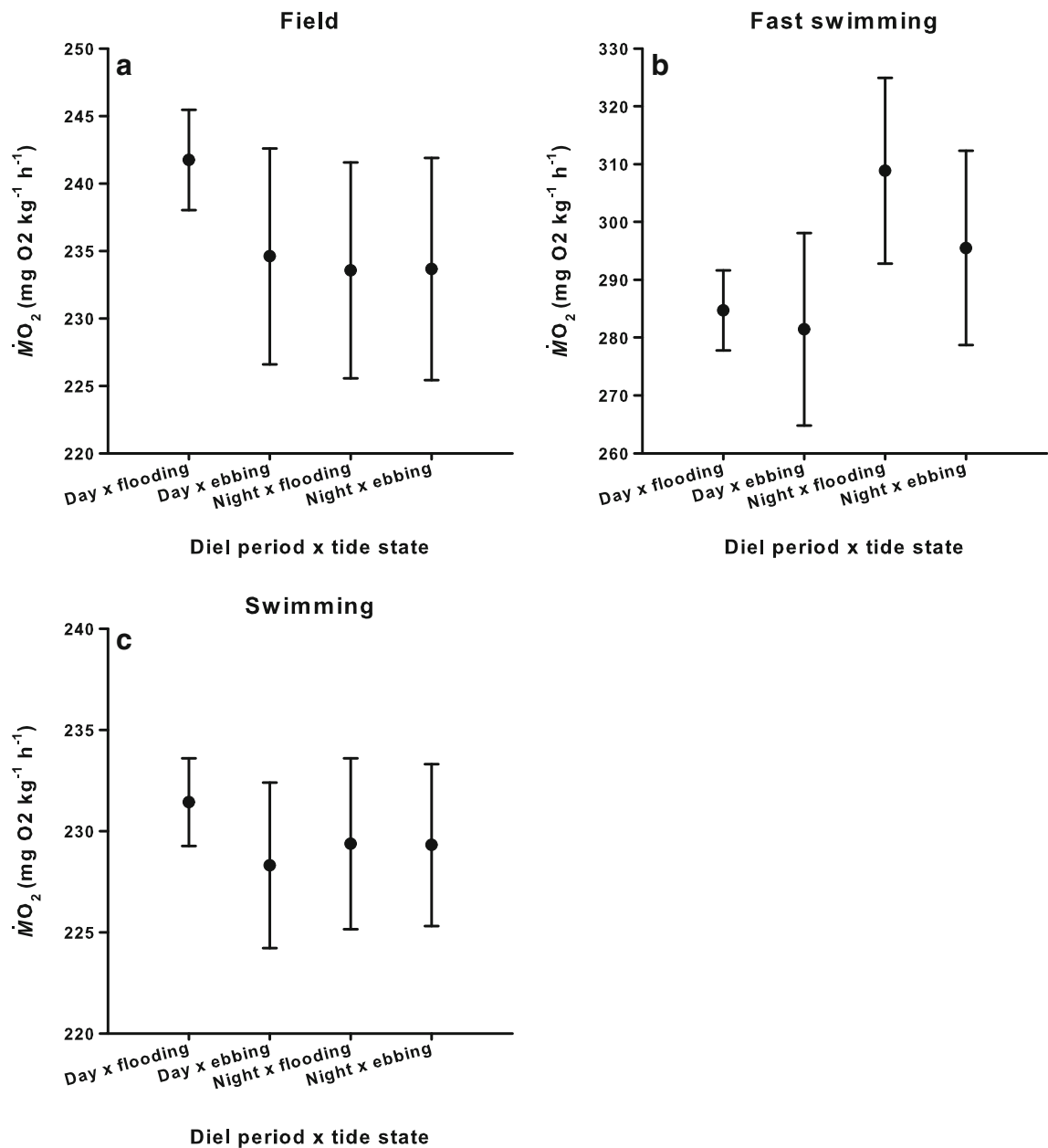
Fig. 3 Oxygen consumption rates ($\dot{M}O_2$) estimated for lemon sharks in situ at day and night, and during flooding and ebbing tides. Overall field $\dot{M}O_2$ (**a**), fast swimming $\dot{M}O_2$ (**b**), and swimming $\dot{M}O_2$ (**c**) are presented. Data are presented as means ±95.0% credible interval

correlations between the occurrence of specific behaviors and energy use were not explicitly investigated (Murchie et al. 2011; Brownscombe et al. 2014, 2017). In fact, for bonefish and other ectothermic species (e.g., *Hydrophis* spp.), variation in activity levels and energy expenditure is observed at temporal (diel, tide, season) and even spatial scales (Brownscombe et al. 2017; Udyawer et al.

2017). As such, the influence of diel and tidal variation in behavior on overall activity costs for sharks in the present study could itself be considerably different to sharks observed at different seasons (e.g., winter) or habitats (e.g., sandflats, lagoons). Indeed, the specific conditions of an animal's habitat can have implications for relationships between physiology and behavior, or in this case,

oxygen consumption and swimming (Killen et al. 2013). Therefore, studies with the goal of generating in situ observations of behavior and physiology with remote sensing techniques ought to consider a range of environmental conditions when calibrating sensors against physiological metrics (e.g., temperature, salinity, dissolved oxygen, pH) or when constructing an ethogram, and to analyze data in an ecologically relevant spatiotemporal context (Cooke et al. 2016; Metcalfe et al. 2016; Treberg et al. 2016). Furthermore, studies that incorporate estimates of anaerobic and digestive costs will be necessary for generating comprehensive energetics models.

Juvenile lemon sharks at Cape Eleuthera appear to be most active during the day. Lemon sharks engaged in burst and fast swimming most often, and had the highest $\dot{M}O_{2Field}$, during daytime flooding tides, indicating that wild lemon sharks are most active during the day. These data agree with our mesocosm study, and suggests that diel period and tide state are important drivers of activity for Cape Eleuthera's lemon sharks (Bouyoucos et al. 2017b). However, these data contradict previous work in juvenile lemon sharks from around the Caribbean and Florida Keys that suggest lemon sharks are either crepuscular or nocturnal (Tricas and Gruber 2013). Specifically, it has been suggested for some populations that documented increases in activity associated with feeding occur during twilight (Tricas and Gruber 2013). Activity patterns in fishes are also known to be plastic, and transitions between diurnal, nocturnal, and crepuscular active periods can be driven by temperature, predation risk, food availability, and intraspecific competition (Reebs 2002). Indeed, regional and local behavioral plasticity between subtropical shark populations has been documented for other species, such as *Carcharhinus perezi* (Brooks et al. 2013). In our system, the high occurrence of burst swimming and fast swimming during daytime flooding tides suggests either that sharks are actively feeding as they, or their prey, return to Kemps Creek (Harborne et al. 2016), or that animals are actively avoiding potential predators as the creek becomes more accessible by larger fishes (Guttridge et al. 2012). Given that lemon sharks at Cape Eleuthera are less active during all other day and tide combinations (i.e., more swimming and less burst and fast swimming), perhaps these sharks are not asynchronous feeders, as has been suggested for Bimini's population (Cortés and Gruber 1990). However, the context of sharks' diel behavior is likely also explained by habitat,

where activity levels of other species are known differ within heterogeneous environments (Brownscombe et al. 2017; Udyawer et al. 2017). Indeed, tidal creek and lagoon ecosystems likely vary sufficiently to support intraspecific variation in diel activity levels. As such, these data add to the body of work highlighting variation in diel activity for wild lemon shark populations, although without offering evidence of any specific ecological drivers. Furthermore, these data suggest that, in the context of other studies, diel activity levels and cycles might differ considerably for coastal elasmobranch species between populations of conspecifics. Species occupying a diversity of habitat types should, therefore, not be assumed to have consistent diel rhythms for activity.

In the wild, lemon sharks were predicted to devote a third of their AS to routine swimming activity. Juvenile lemon sharks, on average, consumed oxygen at 32.3–35.6% of their AS; swimming occupied 30.7% of the available AS 77.8% of the time, and fast swimming occupied up to 63.3% of their AS. Lemon sharks were estimated to swim at a comparatively lower percent of their AS than obligate ram-ventilating species (e.g., *Sphyrna lewini*, *C. plumbeus*), which is unsurprising given these difference in respiratory mode and, therefore, minimum $\dot{M}O_2$ (or standard metabolic rates; SMR) between these species (Lowe 2001; Dowd et al. 2006). Comparatively, bonefish have a higher estimated SMR than lemon sharks at comparable temperatures, and individuals observed in this study's mesocosm exhibited used 40.0–60.0 of their AS to support routine activity (Murchie et al. 2011; Nowell et al. 2015; Bouyoucos et al. 2017b). Species that use a relatively small portion of their AS to support routine swimming activity should have a relatively higher capacity for taking on additional metabolic demands, because swimming activity is the most costly and variable component of the metabolism in active shark species (Lowe 2001). Indeed, fishes that spend relatively more time using a high portion of their AS may experience greater risk of mortality as a consequence of depleted energy reserves or improper allocation of energetic substrates (Priede 1977). Maintaining a large available AS could be beneficial or detrimental for young lemon sharks. To their benefit, maintaining a high aerobic capacity could preserve some aerobic capacity when experiencing an increase in $\dot{M}O_2$ following a meal (specific dynamic action; Norin and Clark 2017) or exercise (excess post-exercise oxygen consumption; Bouyoucos et al. 2017b, 2017c), and may support the claim that young lemon sharks are physiologically

resilient to capture stress (Danylchuk et al. 2014). Conversely, maintaining a high aerobic capacity may support increased food intake and, therefore, high growth rates that can be selected against in some lemon shark populations (Auer et al. 2015; Hussey et al. 2017). However, additional research is warranted to determine how variation in environmental conditions affects AS and the cost of oxygen-demanding activities, because lemon shark populations should be expected to experience changes in performance owing to climate change.

In conclusion, this study did not present a clear physiological basis (i.e., oxygen consumption rates) underlying swimming behaviors observed in situ for juvenile lemon sharks. It has been suggested that environmental stressors alter relationships between physiology and behavior (Killen et al. 2013), so it is likely that variables that were unaccounted for in the field (e.g., predator-prey dynamics) may have influenced behaviors. Specifically, we predicted that lemon sharks would have rested most frequently because this behavior exhibited the lowest oxygen consumption rate. However, our prediction was supported for active swimming behaviors (swimming, fast swimming, burst swimming), as this was expected from activity data for other ram-ventilating species (Lowe 1996; Gleiss et al. 2010). Thus, these data do not contribute much to a basic understanding of the activity and oxygen consumption of lemon sharks in the wild (Bouyoucos et al. 2017b). However, these data are relevant to linking behavioral modifications to changes in energy use (Barnett et al. 2016; Bouyoucos et al. 2017c), that shows much promise for addressing conservation issues in fishes.

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