

CASE REPORT

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Interspecific foraging association of a nurse shark (*Ginglymostoma cirratum*) with bottlenose dolphins (*Tursiops truncatus*)

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Abstract

Animals sometimes forage in mixed species groups, where an individual of a “follower” species actively trails a foraging individual of another “nuclear” species to benefit from the latter’s foraging strategy. Here, we report on a serendipitous observation of a large, benthic, reef-associated predator, the nurse shark (*G. cirratum*) following a pod of bottlenose dolphins (*T. truncatus*) in an apparent attempt to feed on benthic prey disturbed by dolphin foraging. Data from a shark-borne camera, accelerometer, depth, and temperature datalogger package show the nurse shark following the dolphin pod for a period of 15 min and performing multiple, rapid vertical ascents from a depth of 24 m to near the surface following dolphins. The shark performed gliding descents behind dolphins back to the benthos and repeatedly swam through clouds of sand that were produced from dolphin crater feeding behavior. The dolphins appeared to ignore the shark except for three occasions when they struck the shark in the head with their caudal flukes. The shark eventually appeared to locate a benthic prey item as it turned sharply, stopped swimming, and performed what appeared to be suction feeding near the bottom, with clouds of sand rapidly expelled from its gills. This is the first report of rapid vertical ascents and interspecific foraging in a nurse shark.

Introduction

Finding and capturing heterogeneously distributed prey is a constant challenge for predators, and the presence of competitors is often used to signal prey availability [1, 2]. This transfer of information is known as local enhancement and can lead to group or social foraging [1, 2]. Group foraging is often more efficient (decreasing search times, increasing capture probability) for some or all members of the group and can also reduce predation risk while foraging [3]. In marine ecosystems, predators have a complex three-dimensional space to search for food and, where prey is abundant, there is often a high density

and diversity of predators that are competing for food as well as facilitating prey capture.

Following behavior is a common mechanism of group cohesion and is used during interspecific foraging. During this behavior, a “follower” individual tracks a focal “nuclear” individual as it forages [4]. The goal of the follower is to capitalize on prey that are flushed out by the nuclear animal. For example, ant birds (family Formicariidae) in the tropics follow swarming groups of ants to capture flushed out prey [5, 6] and various teleost species commonly follow octopus or moray eels as they forage over coral reefs [4, 7, 8]. The follower species receives a benefit, but for the nuclear species these associations can either result in benefit (mutualism), no effect (commensalism), or harm (parasitism; [9]).

Here, we document a prolonged interaction between a nurse shark (*G. cirratum*) and a pod of bottlenose dolphins (*T. truncatus*; Additional file 1: Video S1), two commonly observed megafauna species in the Florida

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Keys [10–12]. The nurse shark is a large (>2 m), common coastal species in southern Florida and is frequently observed resting near coral reefs solitarily or in groups during daylight hours [11]. As a benthic shark species, they have a low metabolic rate [13] and are thought to be sedentary and ill-adapted for efficient swimming [11]. However, Pratt et al. [14], have reported individuals making annual migrations over 600-km roundtrip, suggesting that this species is a capable swimmer. As a generalist predator, the nurse shark diet contains both vertebrate and invertebrate prey, which are captured through suction feeding [15] that is presumed to occur mainly at night, with no reports of group foraging between individuals [11].

In contrast, bottlenose dolphins are strong swimmers that forage both individually and in cooperative social groups [16, 17]. While dolphins are commonly recorded with sharks and tuna in fisheries data [18], the degree of group foraging and mechanism of cohesion in these interspecific groups is not understood. Traditionally, the relationship between sharks and dolphins is viewed as predator–prey; however, sharks and dolphins are also recognized as competitors [19]. Bottlenose dolphins and nurse sharks have considerable diet overlap with shared teleost and invertebrate prey items [11, 19, 20]. Here, we present the first evidence of putative interspecific foraging between a nurse shark and a pod of bottlenose dolphins.

Methods

A 235-cm total length male nurse shark was tagged on 26th June 2021 in the Dry Tortugas National Park, Florida, where nurse sharks aggregate and mate in the shallows every summer [21–23]. The animal was captured in shallow water using a large dip net, and restrained in the shallows for measurement, sampling, and tagging [14]. A custom datalogger package was applied to the dorsal fin that contained an accelerometer, depth, temperature datalogger (Axy-depth, Technosmart, Rome, Italy), a VHF transmitter (MM 180b, Advanced Telemetry Systems, Isanti, MN) as well as a custom-made digital camera logger with a 120-degree lens (oriented vertically) recording at 1280 × 720 pixels and 20 frames per second. The float and camera logger were designed and built by the lead author and attached to the shark's first dorsal fin with zip ties connected in series to a 1-day galvanic timed release (Undersea Release Devices, New Zealand) following methods described in Whitmore et al. [24]. The animal was released at 13:54 h and was directly observed swimming in the shallows for several minutes before it disappeared into deeper water. After corrosion of the galvanic link, the datalogger floated to the surface and

was recovered with VHF telemetry following methods described in Lear and Whitney [25].

The datalogger package stayed on the shark for 13.3 h, all of which were recorded by the acceleration, depth, temperature logger, with the first 9.2 h also recorded by the camera logger before the memory filled. All reported results were documented by the camera logger and corroborated by the acceleration, depth, and temperature logger where appropriate. Data analyses were conducted in R (version 4.0.4). Static and dynamic acceleration were separated from the raw acceleration using a 3-s running mean and were used to calculate the overall dynamic body acceleration (ODBA). Tailbeat frequency was calculated using a continuous wavelet transform of the dynamic sway axis using the *biwavelet* package [26].

Results and discussion

Camera logger video showed that, upon release, the shark remained in shallow water (<3 m) for 40 min where it encountered a variety of species in the shallows, including a Caribbean reef shark (*C. perezii*), a lemon shark (*N. brevirostris*), several juvenile green sea turtles (*C. mydas*), and multiple other nurse sharks. Over the next four hours the shark intermittently rested and swam, utilizing both shallow and deeper (~20 m) habitats. Four and a half hours after it was tagged the shark gradually descended through reef and soft coral habitat until it reached an unconsolidated sediment bottom habitat (sand/mud) in approximately 24 m of water.

After swimming along the bottom at this depth for 13 min, the shark swam through a cloud of disturbed sediment, then made a rapid ascent toward the surface, at which point the caudal fluke of a bottlenose dolphin could be seen several meters ahead (Fig. 1a). The shark followed the dolphin near the surface for 52 s before the dolphin descended to the seafloor (Table 1). The shark immediately changed its pitch angle and began a passive gliding descent (few or no tailbeats; Fig. 1b).

Once on the bottom, the shark continued behind the dolphin, swimming along the seafloor. After 10 s, the dolphin was observed in a vertical orientation with its rostrum pressed into the seafloor, indicative of crater foraging (Fig. 1c). Upon the dolphin's ascent to the surface, the shark ascended to the surface for a second time where it began to swim with a pod of at least four dolphins (Fig. 1d).

After one minute at the surface, a dolphin began descending to the seafloor, and the shark immediately descended. Nine seconds into the shark's descent, a dolphin came into view (Figs. 1e and 2) and appeared to strike the shark with its caudal fluke. Five seconds later, a second dolphin was observed in the camera frame and struck the shark with its caudal fluke. Both strikes were

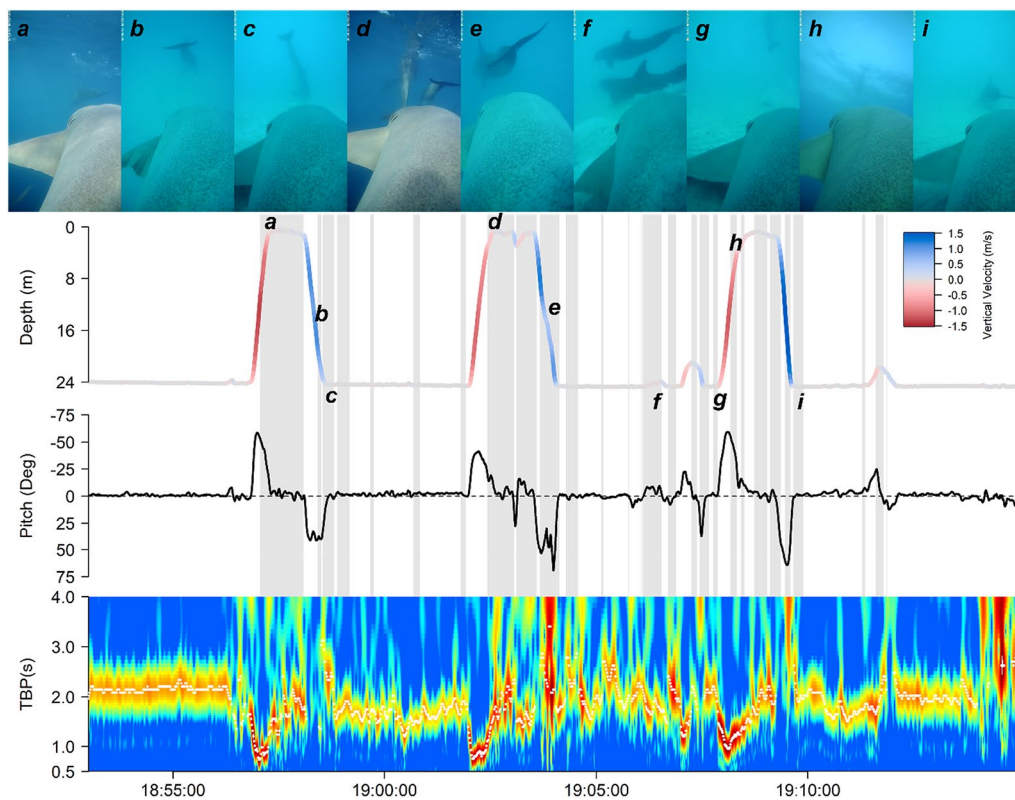


Fig. 1 Overview of nurse shark interaction with bottlenose dolphins. The depth (color coded by vertical velocity), body pitch and tail beat period spectrogram (warm colors represent increased signal strength, white points represent estimates of tail beat period), before during and after interacting with the dolphins. Grey vertical shading represents time when dolphins were visible in the camera frame. Video frames were extracted (a–i) and show dolphins at the surface (a, d, h), descending (b, e) and on the bottom (c, f, g, i), with letters corresponding to the portion of the depth plot labeled with each letter. A dolphin can be observed crater feeding (c) and preparing to strike the shark with its caudal fluke (e)

recorded as abrupt acceleration spikes with the shark subsequently rolling to one side (Fig. 2), and the second strike was forceful enough to bend the pectoral fin so that the ventral side was visible to the camera. Despite these two strikes, the shark continued following the dolphins as they swam along the seafloor. Approximately 17 s later, two dolphins passed in front of the shark and one of them rolled on its side and struck the shark with its fluke (Fig. 1f). The shark continued swimming with these dolphins after being struck. After a 4-min period of swimming along the bottom (bottom phase, Table 1) a dolphin could be seen swimming to the surface and the shark subsequently began its third ascent (Fig. 1g). The shark remained at the surface with the dolphins for 51 s (Fig. 1h) before descending with the dolphins to the seafloor (Fig. 1i). Two minutes after the shark descended to the seafloor, the dolphins were visible on the video for the last time. Two minutes later the shark appeared to suction feed; it stopped swimming and repeatedly flexed its gill slits in a forceful manner, generating a large sediment cloud. This behavior lasted for 40 s before the shark

continued swimming. Thirty-three minutes after this putative foraging event and 35 min after the dolphins last appeared in the video, the shark swam back into shallower (< 13 m) reef habitat for the remainder of the 13.3 h datalogger deployment.

The shark was associated with the dolphins for a total of 15 min (first to last sighting of a dolphin on the camera logger video). During this period, dolphins were observable in the camera frame 47.2% of the time. Vertical movements to and from the surface appeared to be initiated by the dolphins. On two of the three ascents, and on all three of the descents, a dolphin was observed starting an ascent or descent immediately before the shark did. The shark appeared to be directly following the dolphins as they were within the camera frame for the majority of time during the descents (39, 94, 70% visible, Table 1).

During each of the three ascents the nurse shark displayed extreme body pitch (-58 , -41 , -59 degrees), vertical velocities (-1.3 , -1.1 , -1.2 ms^{-1}) and tail-beat frequencies (max = 1.3, 1.3, 1.3 Hz) (Table 1). Similarly, during descents, the shark also displayed extreme

Table 1 Chronology of nurse shark behavior and association with bottlenose dolphins, including the shark's overall dynamic body acceleration (ODBA), tailbeat frequency, body pitch, vertical velocity, and percent of time that dolphins were visible in the camera frame for each behavioral period

	Start time	Duration (s)	ODBA (mean \pm SD)	Tailbeat frequency (Hz)	Pitch (deg)	Vertical velocity (ms^{-1})	Dolphins visible (%)
Control	2021-06-26 18:26:53	1800	0.13 \pm 0.07	0.45	- 1.6 (- 21 to 23.7)	0 (- 0.2 to 0.3)	0
Ascent	2021-06-26 18:56:53	23	0.35 \pm 0.16	1.11	- 45.4 (- 58.8 to - 13.8)	- 1.0 (- 1.3 to - 0.2)	57
Surface	2021-06-26 18:57:16	52	0.17 \pm 0.08	0.60	- 2.5 (- 13.8 to 15.3)	0 (- 0.4 to 0.3)	96
Descent	2021-06-26 18:58:08	28	0.11 \pm 0.07	0.39	37.9 (9.7 to 41.5)	0.9 (0.2 to 1.1)	39
Bottom	2021-06-26 18:58:36	205	0.11 \pm 0.06	0.59	- 1.9 (- 13.5 to 9.7)	0 (- 0.2 to 0.2)	27
Ascent	2021-06-26 19:02:01	29	0.36 \pm 0.15	1.14	- 33.9 (- 41.5 to - 13.5)	- 0.8 (- 1.1 to - 0.2)	21
Surface	2021-06-26 19:02:30	63	0.19 \pm 0.09	0.59	- 4 (- 19.3 to 27.7)	0 (- 0.3 to 0.4)	98
Descent	2021-06-26 19:03:33	31	0.29 \pm 0.26	0.43	45.5 (6.7 to 69.3)	0.7 (0.1 to 1.2)	94
Bottom	2021-06-26 19:04:04	230	0.13 \pm 0.08	0.51	- 0.5 (- 22.8 to 37.6)	0 (- 0.4 to 0.5)	44
Ascent	2021-06-26 19:07:54	32	0.31 \pm 0.14	0.83	- 41.9 (- 59.4 to 7.7)	- 0.7 (- 1.2 to - 0.1)	38
Surface	2021-06-26 19:08:26	51	0.15 \pm 0.07	0.54	- 3.2 (- 15.6 to 13.8)	0 (- 0.3 to 0.2)	69
Descent	2021-06-26 19:09:17	20	0.12 \pm 0.07	-	50.2 (13.8 to 64.3)	1.2 (0.2 to 1.6)	70
Bottom	2021-06-26 19:09:37	136	0.11 \pm 0.06	0.55	- 2.5 (- 25 to 16.8)	0 (- 0.3 to 0.6)	26
Control	2021-06-26 19:15:09	1800	0.10 \pm 0.05	0.49	- 1.5 (- 10.3 to 6.2)	0 (- 0.1 to 0.1)	0

Numbers for pitch and vertical velocity are formatted in median (min-max). Controls represent the 30-min period before and the 30-min period after the interaction with the dolphins

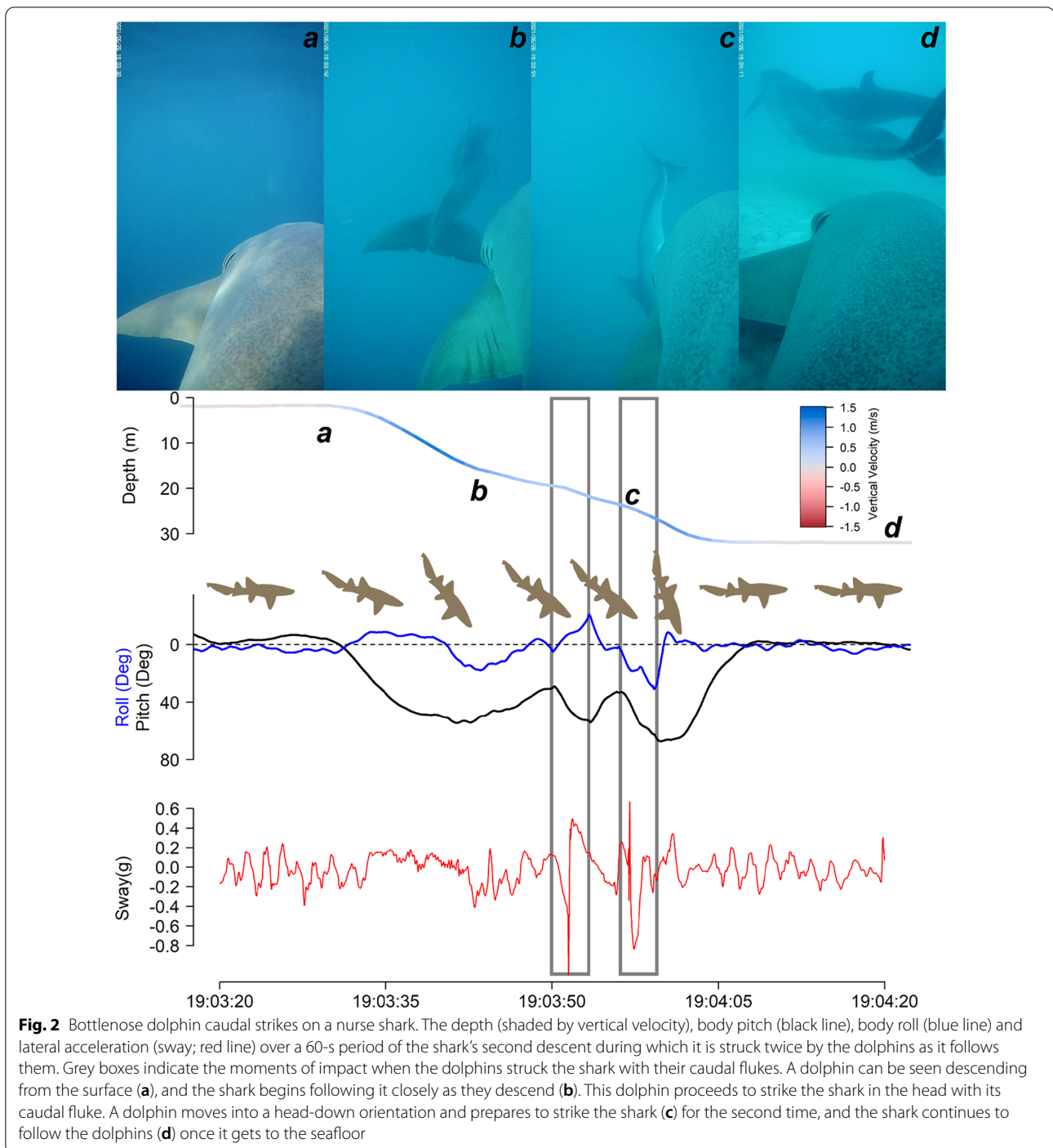
maximum body pitch (41, 69, 64 degrees) and vertical velocities (1.1, 1.2, 1.6 ms^{-1}) (Table 1). Throughout the rest of the shark's deployment, body pitch ranged from - 30 to 38 degrees, while vertical velocity ranged from - 0.3 to 0.45 ms^{-1} . The vertical velocity of these ascents and descents is similar to that of diving dolphins [27] and represent a departure from nurse shark routine behavior. Considering there was no evidence of surface foraging, the shark likely followed the dolphins to the surface to maintain contact with them as dolphins were almost always visible while the shark was close to the surface (96, 98, 69%, mean = 82.7%, Table 1). Although dolphins were only visible 28% (27, 44, 26%, Table 1) of the time in which the shark was swimming along the seafloor, this was likely due to reduced field of vision, lower light availability, and reduced visibility caused by clouds of sediment from the dolphins' foraging. We believe the shark was in close proximity to the dolphins throughout this time.

The camera logger recorded at least three instances of dolphins benthically foraging in a behavior known as crater feeding, common of bottlenose dolphins in the Florida Keys and The Bahamas [28]. During crater feeding, a dolphin uses echolocation to probe the seafloor for organisms beneath the sediment; when a dolphin locates a prey item, it buries its rostrum into the sediment in an attempt to capture it, leaving behind a crater [28]. This behavior generates large visible clouds of

stirred sediment which are known to attract numerous follower species in reef habitats [8].

We believe that the nurse shark was following the dolphins to capitalize upon prey items that were displaced by the dolphins foraging, indicating nuclear following behavior. Previous evidence of sharks employing this strategy is limited and largely anecdotal. For instance, oceanic whitetip sharks (*C. longimanus*) have been observed following pilot whales (*G. macrorhynchus*) in a presumed foraging association [29–31]. Another study has quantitatively documented interspecific foraging with grey reef sharks (*C. amblyrhynchos*) following whitetip reef sharks (*T. obesus*) while they foraged in holes on a coral reef in Fakarava atoll, French Polynesia [32]. As generalist predators [11, 33], nurse sharks are capable of ingesting a diversity of displaced organisms, a common characteristic among follower species [4].

During the 15-min period in which it was associated with the dolphins, the shark showed the highest average ODBA (0.158 g) of any period during its deployment. It was 27% higher than the shark's routine swimming ODBA and approximately double the average ODBA over the shark's entire deployment. This high activity level, coupled with the vertical movements displayed by the shark, suggests considerable effort to maintain proximity to the dolphins. Despite being repeatedly struck by dolphins, the shark continued to follow them, suggesting that the shark was attempting to maintain contact.



Dolphins have several characteristics including echolocation, social foraging, and lateral transfer of knowledge that allow them to use group tactics to find patches of high prey density [34]. It therefore seems likely that the nurse shark was attempting to take advantage of these behaviors and maximize its own foraging efficiency in anticipation of a substantial prey reward.

Although this foraging association lasted only 15 min, most nuclear associations on reefs last less than one minute, with the longest following associations lasting 18 min [4]. Circumstantial evidence suggests that the nurse shark was tiring by the end of the associative behavior. On its last dive, the shark had a slower ascent, a faster descent, and maintained dolphins in the

camera's field of view for a reduced percentage of time during the bottom phase. As ascents are energetically costly behaviors [35], reducing the ascent rate might be symptomatic of fatigue.

This putative foraging event contradicts a hypothesis put forward by Springer [36] who, based on the observation of thin livers with reduced oil content, suggested that male sharks do not feed during the mating season. Although male nurse sharks show reduced girth and loose skin [23], suggesting loss of mass during the mating season, this may be caused by excessive patrolling and devoting energy to sperm production [22] rather than prolonged fasting.

Our findings highlight the benefit of using video loggers and the importance of placing observed behaviors in context to understand their motivations and drivers of behavior [37]. While traditionally viewed as sedentary animals, these results show that nurse sharks are capable swimmers and can engage in brief periods of highly active foraging.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-022-00305-y>.

Additional file 1. The video clip from the animal borne video logger documenting the entire interaction with the dolphins.

Acknowledgements

We would like to thank the Alliance for South Florida National Parks, the National Park Service and the New England Aquarium for financial support. We thank personnel of the National Park Service at Dry Tortugas and Everglades for logistical support and research permits, particularly G. Simpson, C. Pollack, M. Johnson, C. Hull, T. Howington, T. Gottschall, J. Aronoff and B. Koch. We thank G. Lauder for support and advice, M. Blumstein and R. Knotek for providing helpful comments on early versions of the manuscript and two anonymous reviewers who provided constructive edits that have improved the manuscript.

Author contributions

All authors (CFW, NMW, HLP, TCP) participated in idea conception and data collection. Data analysis was performed by CFW, and manuscript writing was conducted by CFW and NMW. All authors read and approved the final manuscript.

Funding

The Alliance for South Florida National Parks, the National Park Service, and the New England Aquarium provided financial support for this project.

Availability of data and materials

All the data sets are available from the lead author upon request.

Declarations

Ethical approval and consent to participate

All research procedures were reviewed and approved under protocol #2019-05 by The New England Aquariums Institutional Animal Care and Use Committee (IACUC) and protocol #FL_DRTO_Whitney_NurseShark_2021.A2 at the National Park Service.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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Received: 29 June 2022 Accepted: 24 October 2022

Published online: 22 November 2022

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