Preprint, 2010
doi: 10.3354/esr00247

ENDANGERED SPECIES RESEARCH
Endang Species Res

Contribution to the Theme Section 'Biologging technologies: new tools for conservation'

Identifying shark mating behaviour using three-dimensional acceleration loggers

Nicholas M. Whitney[1,*], Harold L. Pratt, Jr.[2], Theo C. Pratt[2], Jeffrey C. Carrier[3]

[1]Center for Shark Research, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida 34236, USA
[2]Center for Shark Research, Mote Tropical Marine Laboratory, 24244 Overseas Highway, Summerland Key, Florida 33042, USA
[3]Department of Biology, Albion College, Albion, Michigan 49224, USA

ABSTRACT: Little is known about the reproductive strategies and mating behaviour of most sharks. Understanding mating behaviour is important as it can determine reproductive success and possibly rates of multiple paternity and fecundity. Additionally, some sharks appear to have specific habitat requirements for mating activities. We tested the utility of a 3-dimensional acceleration logger to identify mating events in free-living nurse sharks *Ginglymostoma cirratum* in an area where behaviours can be observed directly, thus allowing corroboration of acceleration data. Loggers were attached to 4 adult females and were recovered after recording periods of 23.2 to 99.8 h (mean ± SD = 50.0 ± 35.1 h). We used acceleration data to classify several behaviours, including swimming, resting, resting in a surge zone, and mating, with examples of each behaviour confirmed via direct observation. Twenty-six mating events were inferred from acceleration data, ranging from 21 s to 20.1 min in duration (median = 2.22 min), with no events taking place during the nighttime hours between 23:00 and 07:00 h. Four events lasted longer than 9 min and took place during periods when logger-equipped sharks were not acoustically detected within the shallow study site. The similarity in mating behaviours between this and some other species raises the possibility that accelerometry could be used to quantify mating in a variety of shark species. This is the first study to classify mating and other behaviours in free-living sharks from acceleration data.

KEYWORDS: *Ginglymostoma cirratum* · Reproduction · Accelerometer · Mating · Behaviour

INTRODUCTION

Understanding reproductive strategies and mating behaviour is crucial for proper management of marine fish species (Rowe & Hutchings 2003). Shark populations are particularly vulnerable to fishing pressure due to their slow growth, late maturity, and low fecundity (Hoenig & Gruber 1990, Pratt & Casey 1990), and some shark populations have been greatly reduced in recent decades (Musick et al. 2000, Cortés et al. 2002). Despite renewed conservation and management efforts, very little is known about the mating systems of most shark species (reviewed by Carrier et al. 2004). Molecular techniques have emerged to reveal complex reproductive strategies for several sharks, including rates of genetic polyandry that vary widely between species (Saville et al. 2002, Chapman et al. 2004, Feldheim et al. 2004) and between populations within the same species (Daly-Engel et al. 2007, Portnoy et al. 2007). The underlying factors causing these differences are poorly understood, but various aspects of mating behaviour may be the most important determinants of the mating system exhibited by a species or population (Daly-Engel et al. 2007, Portnoy et al. 2007, DiBattista et al. 2008). Unfortunately, the mating patterns of most sharks are unknown, as mating behaviour is difficult or impossible to observe. Thus there has been no method to test behavioural hypotheses regarding mating systems or to determine what physical and biological factors may be required for shark

---

*Email: nwhitney@mote.org

species to mate successfully (Carrier & Pratt 1998, Pratt & Carrier 2007). A device that can record shark mating activities remotely would therefore be an invaluable tool, both for understanding the frequency and diurnal periodicity of mating and for identifying essential mating habitat and environmental conditions.

Acceleration loggers have been applied to a wide range of aquatic species to quantify fine-scale details of swimming dynamics and various behaviours (e.g. Yoda et al. 1999, Tanaka et al. 2001, Kawabe et al. 2003, Kato et al. 2006) and, more recently, have been used to calculate metabolic rates based on an animal's overall dynamic body acceleration (ODBA; Wilson et al. 2006). In sharks, acceleration loggers have been used to quantify activity patterns over several days to weeks in captive whitetip reef sharks *Triaenodon obesus* (Whitney et al. 2007) and measure swimming behaviour and ODBA for periods of several hours in free-living whale sharks *Rhincodon typus* (Gleiss et al. 2009b) and captive lemon sharks *Negaprion brevirostris* (Gleiss et al. 2009a). Since both static and dynamic acceleration can be derived from the total acceleration measured by these devices, they can be used to determine both the body orientation and movements of a logger-equipped subject (Yoda et al. 1999). Such data can provide clear indication of the occurrence and characteristics of several behaviours that may be rare or difficult to observe directly (e.g. Watanabe et al. 2005, Wilson et al. 2008, Shepard et al. 2008, this Theme Section). For example, Tsuda et al. (2006) used accelerometers to classify 8 behaviours associated with spawning in female chum salmon *Oncorhynchus keta* and showed that the occurrence of these behaviours was substantially affected by turbid water runoff after a storm.

Mating behaviour in nurse sharks *Ginglymostoma cirratum*, and some other shark species for which it has been observed, typically consists of a male grasping a female's pectoral fin and attempting to insert one of his paired claspers into the female cloaca (see Pratt & Carrier 2001 for a review). Once a pectoral grasp is attained, the female will often adopt a variety of positions and behaviours to avoid copulating with the male (Carrier et al. 1994, Whitney et al. 2004), or in some cases she will seemingly cooperate and allow copulation to take place (Carrier et al. 1994, Pratt & Carrier 2001). Mating events can last from a few seconds to several minutes and involve behaviours such as rolling, grasping, erratic tailbeats, and arching in unusual postures, including ventral-side-up positions and vertical headstands (reviewed in Pratt & Carrier 2001). For the purposes of the present study, the term 'mating event' is used to refer to all of these activities, regardless of whether or not copulation was achieved.

The goal of the present study was to determine whether acceleration loggers could be used to identify mating behaviour in free-living nurse sharks during their mating season in the Florida Keys. We present acceleration signatures associated with swimming, resting, and mating behaviour, examples of which were confirmed through direct observations. We present a hierarchical decision tree for classifying behaviours based on their acceleration data (e.g. Gleiss et al. 2009a), and we discuss the implications of these findings for future studies of shark reproductive behaviour. We believe that our findings represent the first step toward a broader goal of quantifying mating behaviour in shark species for which it cannot be directly observed.

MATERIALS AND METHODS

Study site and mating behaviour. The Dry Tortugas study site (described in Pratt & Carrier 2007) is a shallow (0 to 1.8 m) marine flat partially surrounded by islands comprising the Dry Tortugas group, Florida, USA. Adult female nurse sharks aggregate in the shallows each year, often shoaling in 1 m of water or less for several weeks during the mating season, with intermittent forays out of the area for hours or days at a time. Males patrol the deeper boundaries of the site, occasionally moving into the shallows to investigate or attempt to mate with a given female (Carrier et al. 1994). Mating typically occurs in the shallows or nearby in slightly deeper (2 to 3 m) water into which males will often attempt to carry a female to improve their chance of successful copulation, which only happens in ~8% of events (Pratt & Carrier 2001). The annual occurrence of this mating aggregation and the animals' use of shallow, clear water make the Dry Tortugas site ideal for capturing and tagging animals and monitoring their behaviour for prolonged periods.

Tag package design and attachment technique. We applied 3-dimensional acceleration data loggers (16 × 108 mm, 35 g, Vemco) to 6 adult nurse sharks (5 female, 1 male) during their mating season in June 2008, and recovered loggers from 4 of the 6 (see Table 1). Loggers were set to record at 5 Hz; other details of logger function are described in Whitney et al. (2007). Each tag package consisted of an acceleration logger, a V16 continuous acoustic pinger tag (Vemco) transmitting once per second, and a timed galvanic release (International Fishing Devices) designed to corrode after a 3 or 7 d period in tropical seawater (Fig. 1). Eyeloops on both ends of the galvanic releases were ground down to nubs (and new holes drilled through them) so they were small enough to pass through the holes in the fin and to be shed after the body of the release had corroded. Tags were held together with elec-

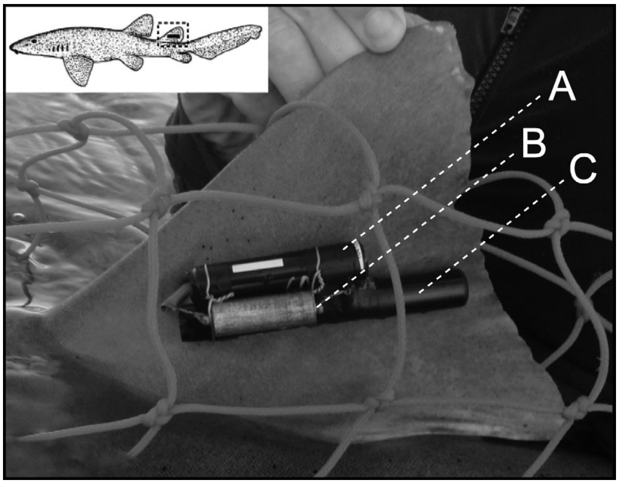


Fig. 1. Tag package fixed to the second dorsal fin of a nurse shark. Lines indicate the (A) acoustic pinger tag, (B) 7 d timed galvanic release, and (C) acceleration logger. Tags are held to the galvanic release with stainless steel locking wire. The tag package is fixed to the fin with steel fishing leader threaded through holes in the fin and fixed to either end of the galvanic release, allowing the entire tag package to fall off once the release has corroded

trical tape and epoxy and held to the galvanic release with stainless steel locking wire (0.8 mm diameter).

Animals were captured in the shallows using large dip nets (see Pratt & Carrier 2005), and logger packages were attached to the second dorsal fin. Small-diameter (28 gauge) steel fishing leader wire was fixed to one end of the galvanic release, passed through a small hole punched in the fin, and returned through a second punched hole in the fin where it was secured to the other end of the galvanic release (Fig. 1). Wire was coated with plastic shrink-tubing to prevent laceration of the fin. This tag package was designed to allow the shark to be acoustically located periodically throughout the study period using an underwater receiver/ hydrophone (DPR-275, RJE), and for the logger to be shed and located on the sea floor after corrosion of the galvanic link.

All animals were also tagged on the first dorsal fin with 2 Jumbotags (Dalton) that were color-coded to allow individuals to be recognized from above the surface and at distances of several meters. Two accelerometer-equipped animals were also tagged with coded acoustic transmitters (V16 R-codes, 180 s mean transmission interval) that allowed their detection via VR2 receivers (Vemco) stationed throughout the study site.

Observations and data analysis. Logger-equipped animals were observed opportunistically throughout the experiments via direct observations from the surface or underwater. A shark's location, behaviour (swimming, resting, mating, etc.), and the time were noted whenever possible, with particular attention given to changes in behaviour likely to be obvious in acceleration data, such as the beginning and cessation of swimming behaviour or the onset of mating events. Logger-equipped animals that could not be seen were occasionally detected by hydrophone, which allowed us to approach them by kayak or snorkeling and note their behaviour.

Recovered loggers were downloaded and the retrieved data were analyzed using Ethographer (Japanese Society of Biologging Science, http://bre.soc.i.kyoto-u.ac.jp/bls/index.php?Ethographer; Sakamoto et al. 2009) with Igor Pro 6.0 wave analysis software and Igor Filter Design Laboratory (Wavemetrics). Body orientation was derived by isolating the static component (due to gravity) of the acceleration signal from the dynamic component (due to animal movement) using a low-pass filter (Tanaka et al. 2001, Kawabe et al. 2003) with the end of the pass band and start of the stop band set to 0.1 and 0.2 Hz, respectively. These band settings were sufficient to exclude tailbeat movements while preserving changes in body orientation (see Watanuki et al. 2005). The resulting static acceleration values thus reflected the device angle of the logger itself, and these values were corrected to animal body angle by subtracting the attachment angle of the logger on the fin. The attachment angle ranged from 4.7 to 20.8°, and was calculated from the mean static acceleration values produced during periods of directly observed horizontal swimming (i.e. no change in depth), when the animal and dorsal fin were in their upright and natural position (Watanuki et al. 2003, 2005). Once corrected, the static component of the surging (longitudinal) axis thereby reflected the animal's body orientation along that axis and could be used to detect changes in pitch. Similarly, the static component of the swaying (lateral) axis reflected the animal's lateral posture and was used to detect rolling. Because of the vertical and horizontal flexibility of nurse shark fins, as well as the posterior location of the second dorsal fin on the body, calculations of body posture from fin-mounted tags should be considered imprecise approximations of trunk posture in this species.

Dynamic acceleration from the swaying axis was derived by subtracting the static component from raw acceleration values, and was used to identify behaviours based on the frequency and amplitude of tail movements. These were visualized using Ethographer to calculate an acceleration spectrogram using continuous wavelet transformation with the Morlet wavelet function, and further quantified using *k*-means cluster analysis to identify local behaviour spectra based on their amplitude and frequency (see Sakamoto et al. 2009, Sato et al. 2009). For analyzing short periods (1 to 5 min) of behaviour, the maximum cluster number was set to 6, as higher cluster numbers were found to artificially separate highly similar spectra that represented the same behaviour. It should be noted that the word ‘amplitude’ as used in these analyses is reflective of signal strength amplitude, and does not directly represent tailbeat amplitude or acceleration amplitude, although both contribute to signal strength (see Sakamoto et al. 2009).

RESULTS

Sharks carried loggers for record durations ranging from 23.2 to 99.8 h (mean ± SD = 50.0 ± 35. 1), and loggers were recovered either by recapturing the animals or via hydrophone-guided recovery of the shed logger after corrosion of the galvanic release (Table 1). Fifty timed behavioural observations ranging from 1 to 78 min in duration were noted, producing 4.65 h of direct observations to corroborate acceleration data. Logger-equipped sharks appeared to behave normally in that they carried out similar behaviours to other female sharks in the area, and we observed no instances of altered swimming or attempts to shed the tag.

Classification of behaviours

Basic behaviours such as swimming and resting were easily identified based on dynamic acceleration from the swaying axis alone, since it coincided with typical side-to-side tailbeat movements (Fig. 2a,b). Cluster analysis of swimming intervals produced a single behaviour spectrum with a large amplitude peak corresponding to tailbeat frequency (Fig. 2e), whereas resting produced multiple low-amplitude spectra, indicating low acceleration and the lack of a clear cyclic signal (Fig. 2f). Direct observation revealed that sharks resting in shallow, turbulent water experienced incidental fin and body movements from wave surge (Fig. 2c), but these movements were clearly different from normal swimming and resting, and produced a single behaviour spectrum with a low-amplitude, low-frequency peak corresponding to the frequency of wave surge (Fig. 2g). More complex behaviours, such as disturbances by researchers or other sharks, could be inferred from sudden, short bursts in tailbeat frequency (TBF) and signal amplitude that were often followed by longer durations of elevated TBF and/or amplitude as the animal fled from the site of the disturbance (Fig. 2d). The 3 phases of such an event (typical swimming, fast-start, and fast-swimming) produced 3 unique behaviour spectra at different frequencies identified by cluster analysis (Fig. 2h).

Mating events were often apparent from the raw acceleration data from all 3 axes and were marked by abrupt changes in acceleration baselines and amplitudes (Figs. 3 & 4a). These were produced by large changes in female body orientation accompanied by tailbeats that were erratic and/or showed high acceleration amplitude interspersed with periods of relative quiescence and/or slow lateral rolling. Changes in orientation were apparent from the static acceleration component of the surge (pitch) and sway (roll) axes as a female moved into a head-down orientation and rolled to one side or the other (Fig. 4b). Patterns in tailbeat activity often indicated females swimming normally before the event, finning erratically or not at all during the event, and swimming with elevated TBF and/or signal amplitude at the end of the event as the logger-equipped female fled the male(s) who had grasped her (Fig. 4c). Cluster analysis of these tailbeat patterns produced local behaviour spectra showing single peaks of high amplitude (at frequencies reflecting TBF) before and after the event, while identifying multiple spectra across a broad range of frequencies that represented the erratic tailbeats and quiescent periods associated with the event itself (Fig. 4d).

Mating events were therefore defined as incidents in which an animal showed changes in pitch or roll of at least 30 degrees while simultaneously exhibiting erratic tailbeats (producing multiple behaviour spectra) and periods of quiescence. The unique characteristics of each observed behaviour allowed us to construct a decision tree from which behaviours were classified based on their acceleration characteristics (Fig. 5). Although behaviours such as diving and foraging/feeding were not observed, we present hypothesized acceleration characteristics of these behaviours that

Table 1. *Ginglymostoma cirratum*. Details of accelerometer experiments for 4 adult female nurse sharks. TL: total length. Coded tag refers to whether the animal was tagged with a V16 coded transmitter (Vemco) that allowed it to be detected by an array of Vemco VR2 acoustic receivers in the study site. Recap.: animal was recaptured and tag package removed; Galv. rel.: tag package was shed after corrosion of galvanic release and recovered via hydrophone

Shark no.	TL (cm)	Duration (h)	Coded tag	Recovery method	Mating events	Mean event duration (min ± SD)
1	263	27.8	–	Recap.	2	3.68 ± 0.01
2	253	49.1	–	Recap.	3	1.82 ± 0.71
3	248	99.8	+	Galv. rel.	7	7.78 ± 6.58
4	249	23.2	+	Recap.	14	2.74 ± 3.27

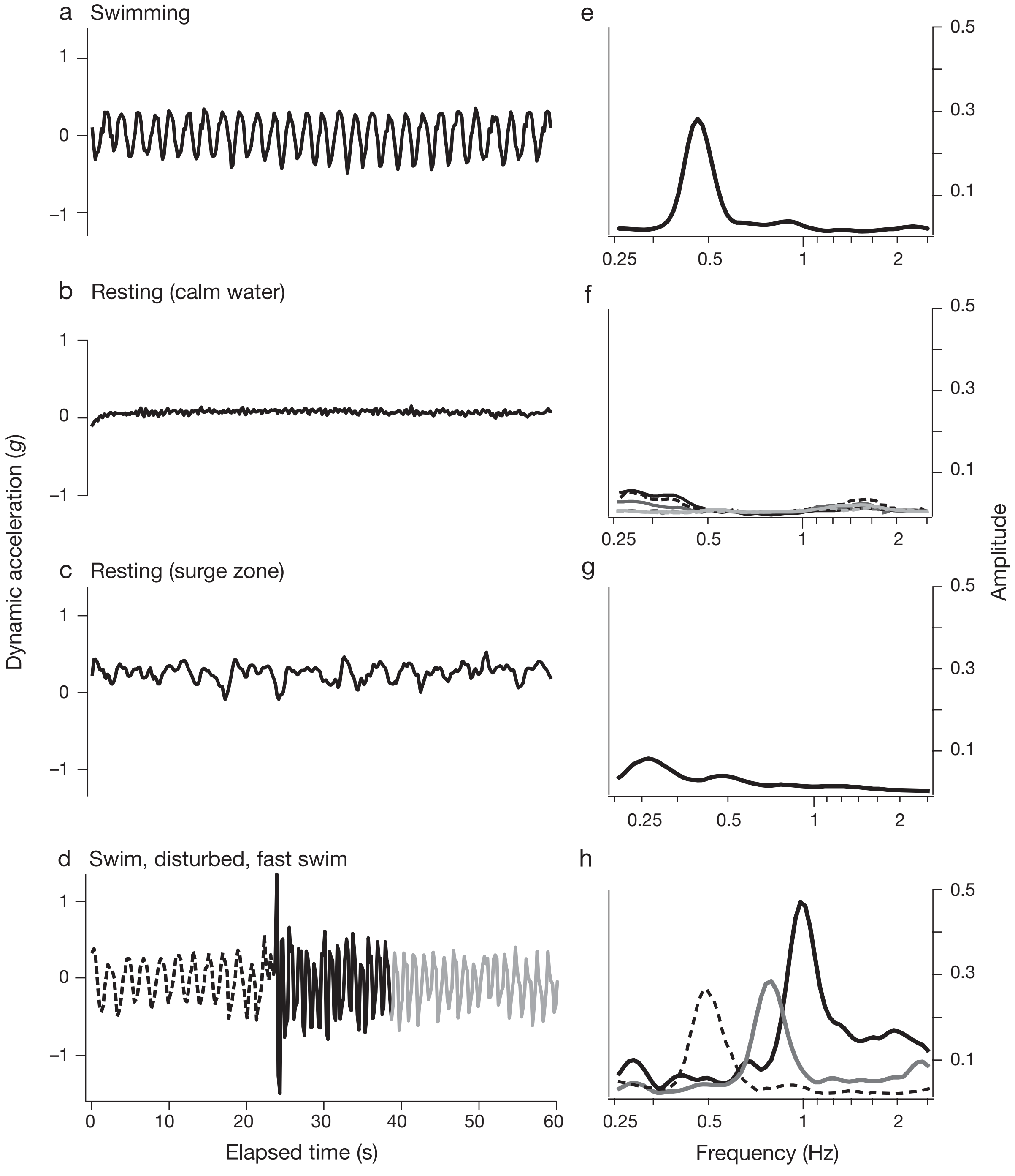


Fig. 2. *Ginglymostoma cirratum*. Dynamic acceleration from the swaying axis only showing signatures associated with (a) swimming, (b) resting, (c) incidental fin movements while resting in a shallow surge zone, and (d) the sudden increase in tailbeat frequency and signal amplitude typical of a disturbance. (e–h) Acceleration spectra produced from each behaviour as identified by *k*-means cluster analysis. Line characteristics in (d) correspond to those of the spectra in (h), whereas line characteristics in (f) indicate the presence of multiple spectra with similar characteristics. All examples shown were confirmed through direct observation from the surface or by divers, and the patterns illustrated were observed in all tagged sharks

we expect to differentiate them from mating and that can be empirically tested in future work.

Two animals (Sharks 2 and 3) occasionally exhibited very short-duration rolls of 4 to 14 s in the midst of swimming or resting. These rolls were not associated with erratic tailbeats and were never directly observed, and therefore were not classified as mating events.

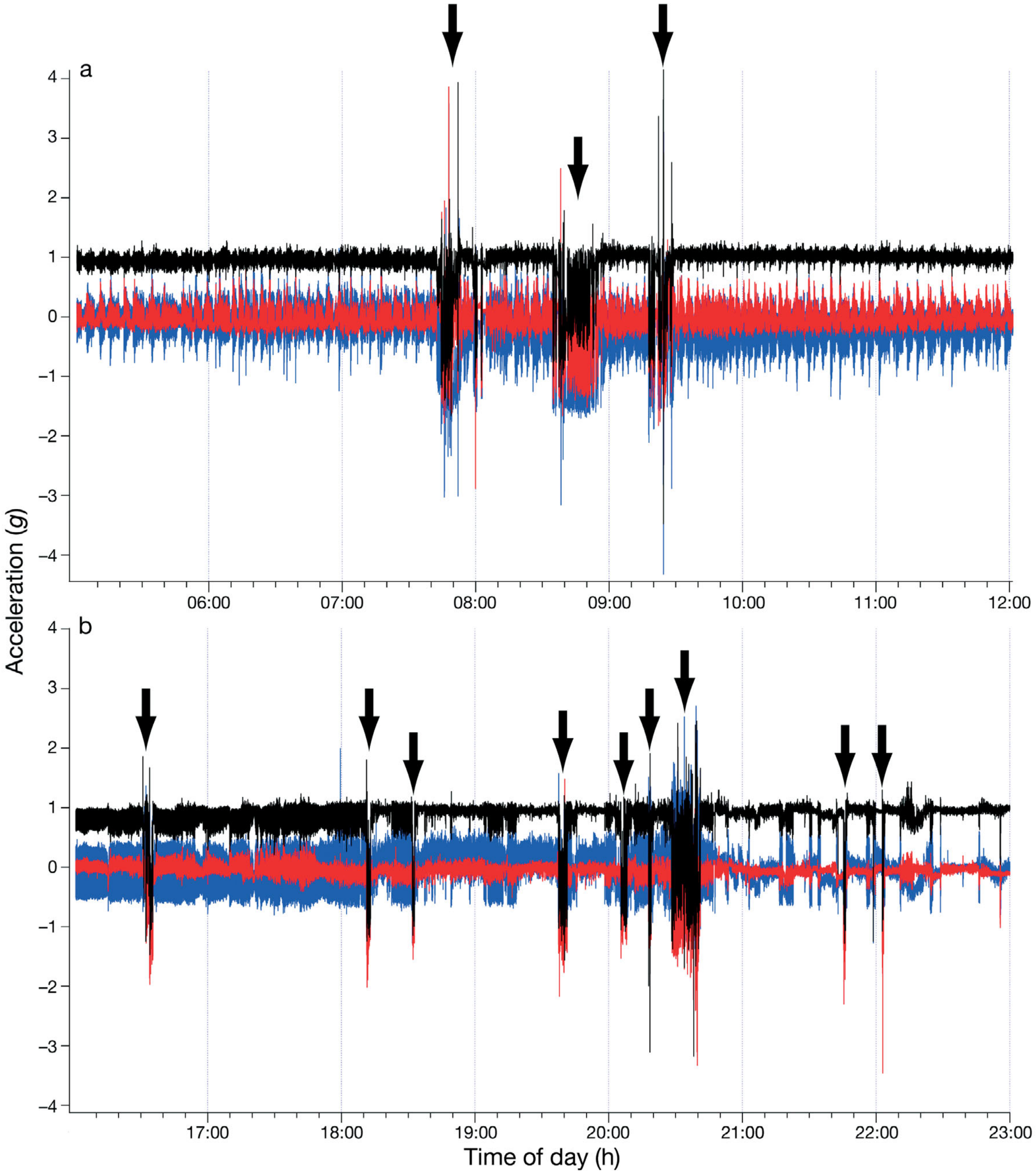
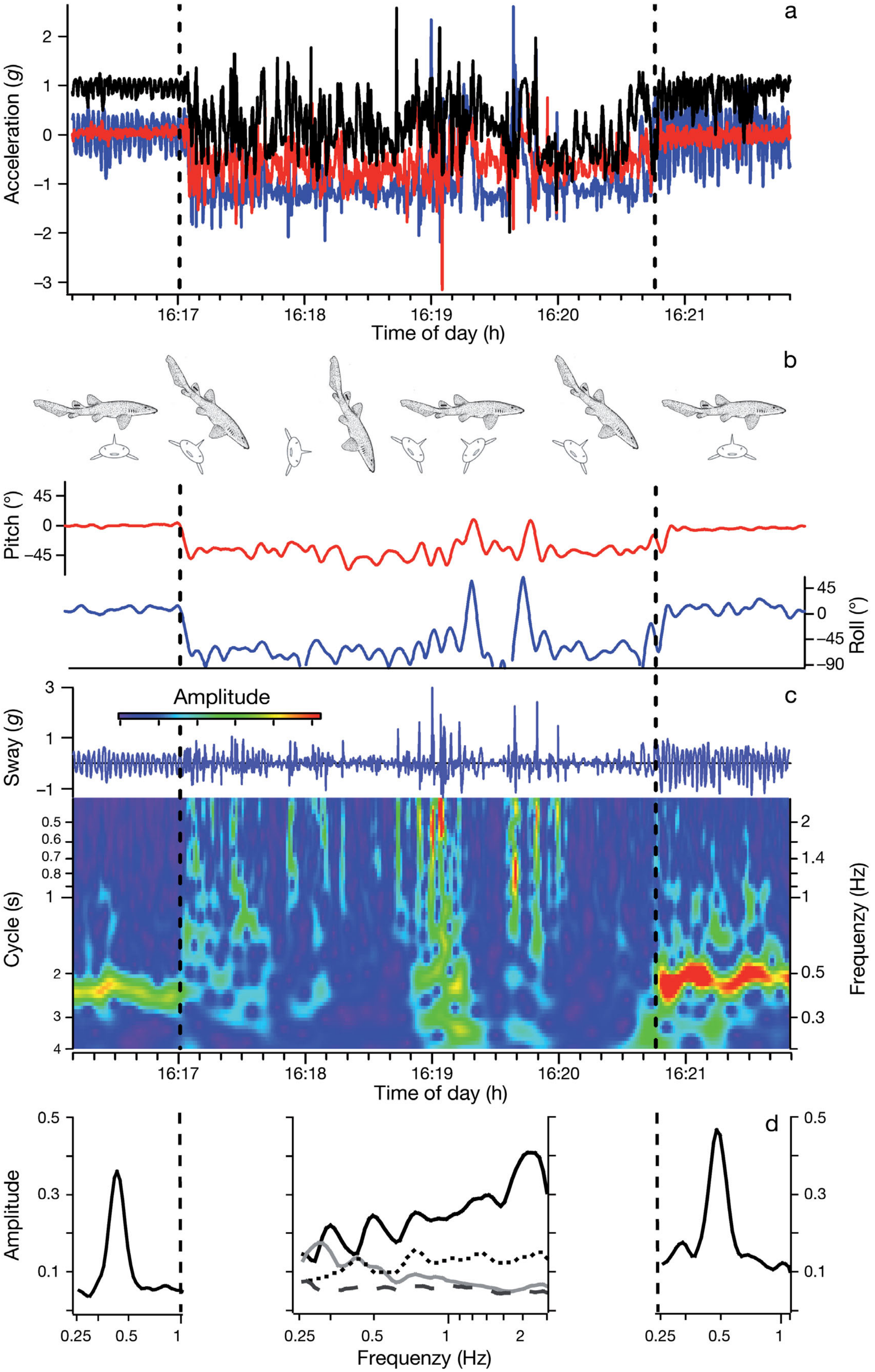


Fig. 3. *Ginglymostoma cirratum*. Seven hours of acceleration data from all 3 axes from (a) Shark 3 and (b) Shark 4, showing several inferred mating events (arrows) for each shark. Blue: swaying (lateral) axis; red: surging (longitudinal) axis: black: heaving (vertical) axis

→

Fig. 4. *Ginglymostoma cirratum*. A mating event between a logger-equipped female and 2 males as represented by the (a) triaxial acceleration data; (b) static component of acceleration (converted to degrees) from the surge (pitch) and sway (roll) axes showing the female moving into a head down pitch of as much as 67° while rolling to 90° and 45° to her left and right, respectively; (c) spectrogram of dynamic acceleration from the swaying (lateral) axis; and (d) behavioural spectra of the event showing typical swimming (tailbeat frequency [TBF] = 0.4 Hz) before the event, sporadic movements across a broad range of frequencies and amplitudes during the event (different line characteristics indicate individual spectra), and faster (TBF = ~0.5 Hz) swimming with high signal amplitude after the event. Vertical dashed lines indicate the start and end of the mating event, respectively. Data trace colours are the same as in Fig. 3. Timing and details of this event were confirmed through direct observation from the surface (i.e. researcher in a kayak)


a
Acceleration (g)
2
1
0
–1
–2
–3
16:17
16:18
16:19
16:20
16:21
Time of day (h)
b
Pitch (°)
45
0
–45
Roll (°)
45
0
–45
–90
c
Amplitude
Sway (g)
3
1
–1
Cycle (s)
0.5
0.6
0.7
0.8
1
2
3
4
Frequenzy (Hz)
2
1.4
1
0.5
0.3
16:17
16:18
16:19
16:20
16:21
Time of day (h)
d
Amplitude
0.5
0.3
0.1
0.25
0.5
1
0.25
0.5
1
2
Frequenzy (Hz)
0.25
0.5
1
0.5
0.3
0.1

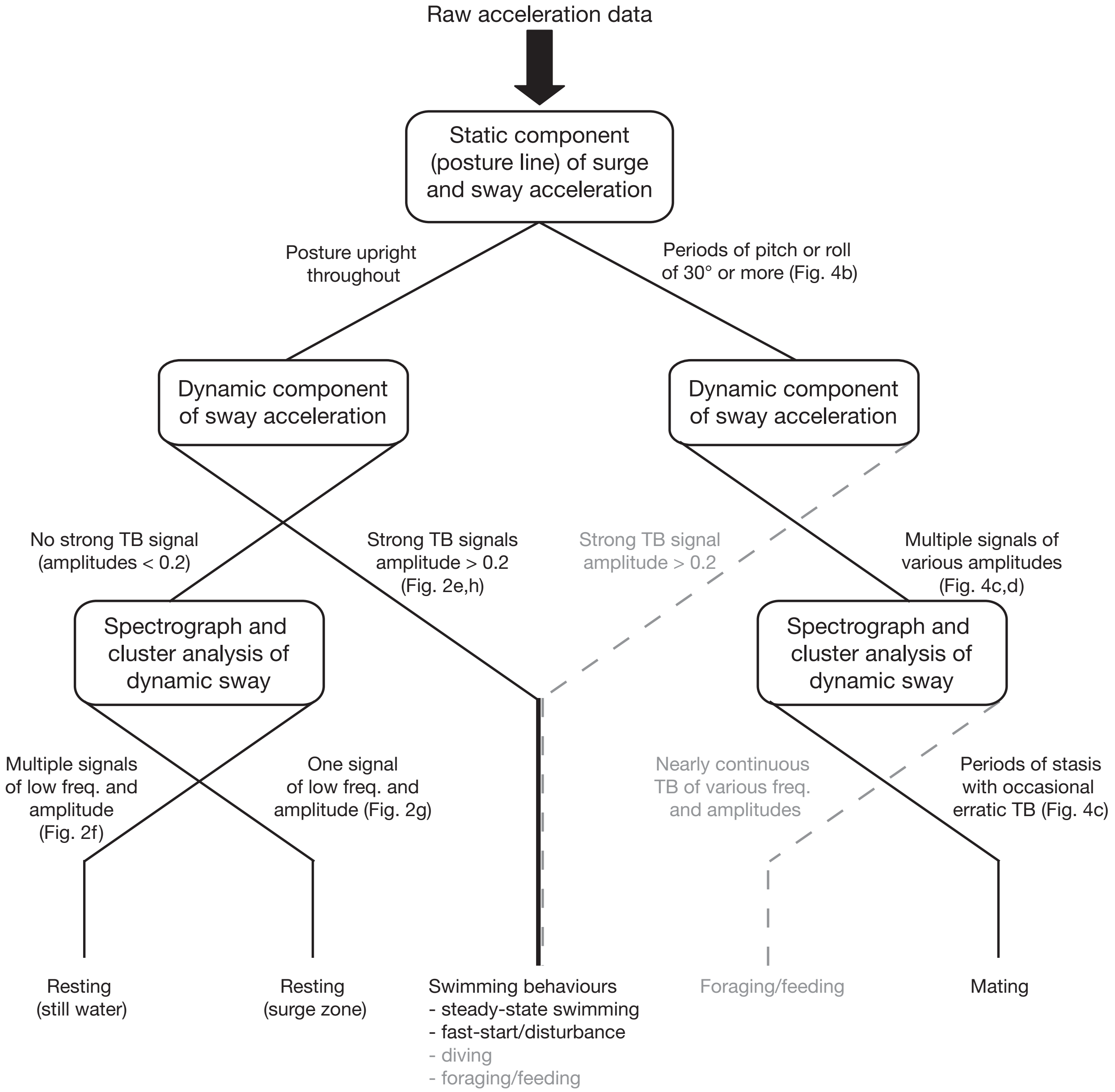


Fig. 5. Tree diagram illustrating the criteria used to classify periods of acceleration data into different behaviours. Grey text and dashed lines indicate hypothesized characteristics of behaviours (diving and foraging/feeding) that were not directly observed. TB = tailbeat

Temporal and spatial distribution of mating events

We classified 26 mating events from acceleration logger data (Table 1), with 2 of these events confirmed through direct observation. Mating events took place throughout daylight hours and occasionally within 2 h after sunset, but no mating was recorded between the hours of 23:00 and 07:00 h, despite all sharks being monitored for at least one overnight interval (Fig. 6). The absence of mating during this period was particularly emphatic for Shark 4, who mated 9 times between 16:30 and 22:30 h one day, then 5 times between 07:00 and 09:30 h the following morning, with no events occurring between the 2 periods. Mating activity for Shark 3 was highly clustered in time, with all 7 events taking place within a single 10 h period of her 99.8 h deployment.

Mating events ranged from 21 s to 20.1 min in duration, with a median duration of 2.22 min. Eighty-one percent of mating events lasted for 6 min or less, with 46 % lasting less than 2 min (Fig. 7). Four events lasted for 9 min or longer, and these often involved periods of

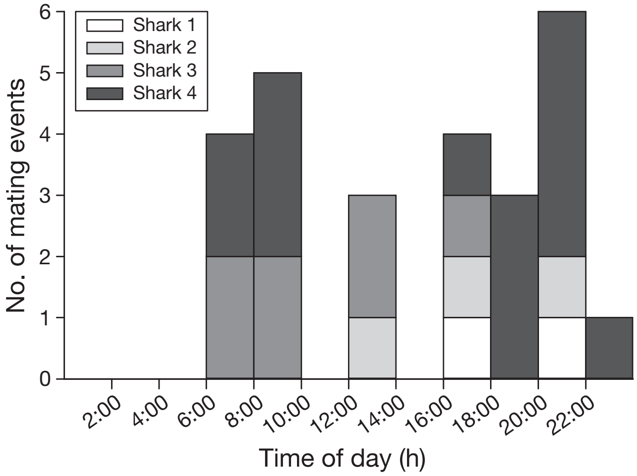


Fig. 6. *Ginglymostoma cirratum*. Time of day for 26 mating events from all 4 logger-equipped sharks

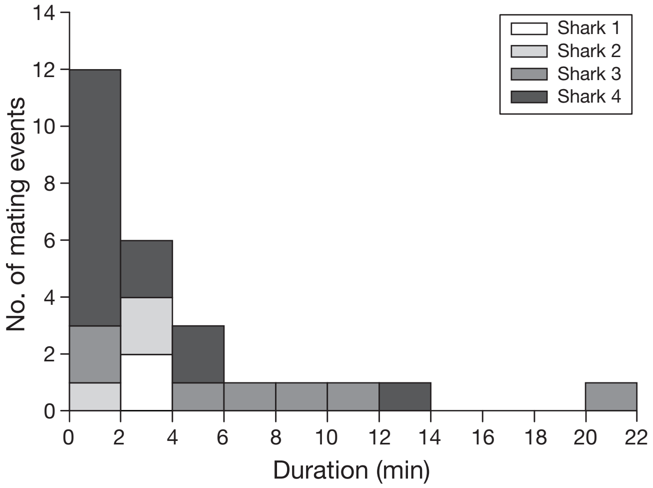


Fig. 7. *Ginglymostoma cirratum*. Event duration for 26 mating events from all 4 logger-equipped sharks

female quiescence lasting up to 1 min or more with her body inverted to various degrees. All of these longer events took place in Sharks 3 and 4, whose coded acoustic tags were not detected in the study area during the time of the events. Some of these may represent instances of multiple males mating the female in quick succession, but we considered a single event to be ongoing until the female exhibited normal swimming or resting behaviour.

The 2 animals (Sharks 3 and 4) carrying coded acoustic tags were detected frequently in the shallows of the monitored study area, but usually not during times of accelerometer-derived mating. Shark 3 was never detected or observed in the study area within 30 min of a mating event, and was detected only twice during the 10 h period in which her mating events took place. She was detected in the study period for several hours each day over the subsequent 41 h of her deployment, during which no mating took place. Shark 4 was detected in the study area within 15 min of 5 (36%) of her 14 mating events, with the other 9 events taking place outside of the monitored area.

DISCUSSION

Classification of behaviours

Acceleration loggers proved highly effective at identifying the changes in movement and orientation associated with mating behaviour in nurse sharks. Although most mating events were apparent from visual examination of acceleration data, the continuous, fine-scale record of shark body movements provided a behavioural context for interpreting each event. The behaviours inferred from acceleration data coincided well with our direct observations and with those from previous studies of this mating aggregation (Carrier et al. 1994, Pratt & Carrier 2001). However, some accelerometer-based behaviours were not directly observed and thus cannot be interpreted with certainty. For instance, the quick rolls exhibited by Sharks 2 and 3 could be indicative of brief, failed attempts by males to roll the tagged females into a mating position, but the lack of erratic tailbeats or evasive swimming (high TBF and/or signal amplitude) behaviour following these rolls appears to contradict this interpretation. These rolls may be intentional attempts to shed the tag package or may indicate the animals being passively rolled by wave action while resting in shallow water. The unique acceleration signature produced by passive fin movements from water turbulence exemplifies the need to collect as many direct observations as possible from logger-equipped animals, and also underscores the benefit of working in clear, shallow water.

Feeding behaviour was not directly observed in any tagged or untagged shark during the present study and could not be inferred from acceleration data. Although all sharks exhibited occasional bouts of fast swimming and abrupt movements, these could have been related to interactions with male sharks or a number of other biotic or abiotic factors. While feeding behaviour in this species can involve head-down orientation and rolling in some cases (H. L. Pratt unpubl. data), we interpreted these behaviours to be mating-related based on their duration, behavioural context, and our direct observations. We hypothesize that feeding behaviour consists of short periods of nearly continuous tailbeats while inverted, whereas mating can last for several minutes and involve long periods of stasis. Similar studies outside of the mating season or on immature sharks are required to identify specific acceleration signatures associated with feeding, and successful feeding events could be confirmed with gastric pH tags (e.g. Papastamatiou et al. 2007).

Temporal and spatial distribution of mating events

The temporal and spatial distribution of mating events indicates a complex suite of behaviours employed by females during the mating season. Vast differences in mating rate between individuals and between days within the same individual lend support to the hypothesis that female attractiveness or willingness to mate fluctuates throughout the mating season, possibly associated with hormone, pheromone, and/or ovulatory cycles (Rasmussen et al. 1992). The fact that most recorded mating events appear to take place outside of the shallow study site may indicate that females swim to deeper water to seek a mate and retreat to the shallows to avoid male harassment. The 4 events with durations greater than 9 min were longer than most of the hundreds of events previously observed in the shallow study site (Carrier et al. 1994, Pratt & Carrier 2001), and appeared to take place outside of the site. Whether these longer events represent advantages involved in mating in deeper water or simply mating at unmonitored shallow sites without disturbance from observers is unknown. Future work incorporating depth-loggers is needed to establish the effect of water depth on mating frequency and duration. Longer events may also be indicative of successful and/or multiple copulations, but this could not be determined from the present study. Further work may allow us to determine copulatory success based on acceleration data or additional devices such as cloacal sensors (Wilson et al. 2004, Metcalfe et al. 2009) that could log clasper insertion events.

Future work and implications for other species

Future accelerometry studies on this population should focus on the development of detailed ethograms and time budgets (e.g. Lagarde et al. 2008) over periods of multiple days. The potential to quantify relative or even absolute measures of energy expenditure using ODBA (Wilson et al. 2006, Gleiss et al. 2009a, Halsey et al. 2009) may also be useful for comparing the energetic investment of males and females during the mating season, which may be highly divergent (Springer 1967). Direct observations and filming of mating behaviour in logger-equipped sharks may also allow specific behavioural components of mating to be classified (Watanabe et al. 2005, Tsuda et al. 2006) based on their acceleration characteristics.

Despite the unique benefits of our study species and location, our methods should be useful for identifying mating behaviour in a wide range of elasmobranch taxa. Although mating has been observed in only a few species, the pectoral grasp, rolling into head-down or ventral-side-up postures, and erratic tailbeating exhibited by nurse sharks have been observed in a number of other species. These include *Triaenodon obesus* (Tricas & LeFeuvre 1985, Whitney et al. 2004), *Hemiscyllium freycineti* (Cornish 2005), *Triakis semifasciata* (Smith 2005), *Heterodontus portusjacksoni* (Powter & Gladstone 2008), *Carcharhinus amblyrhynchos* (Y. Hubert pers. comm.), and *C. melanopterus* (McCauley et al. in press). The discovery of these behaviours in obligate ram ventilating carcharhinids raises the possibility that they may be exhibited by larger coastal species (e.g. *C. plumbeus* and *C. limbatus*) whose populations are targeted by fisheries. Although observations from very large and/or pelagic species are extremely limited (e.g. Francis 1996, Harvey-Clark et al. 1999) and their mating behaviour may differ from small coastal species, such behaviour is still likely to produce highly unique patterns in acceleration and depth data that could be initially confirmed through video or still image loggers (Marshall et al. 2007, Watanabe et al. 2008). Additional advances in logger memory, attachment, and data transmission are also required before accelerometers can be used to quantify long-term behaviour of wide-ranging species, but the groundwork for these studies can be laid now while revealing the short-term behaviour of coastal species. Species for which behaviours can be directly observed to corroborate acceleration data are of seminal importance to the future of this field, as their catalogue of acceleration signatures could be used as a Rosetta stone for interpreting data from more reclusive species.

Regardless of the secondary behaviours involved, all shark copulation requires some period of coupling between male and female through an oral grasp, clasper insertion, or both. Whether the animals are on the sea floor or in the pelagic environment, the act of coupling is likely to reproduce highly unique acceleration signatures that can be clearly differentiated from typical swimming, resting, and feeding behaviours. We believe that our findings represent the first step toward a broader goal of elucidating mating behaviour in shark species for which this mating cannot be directly observed.

Acknowledgements. We thank H. Whitney, D. Webber (Vemco), F. Amador (NGS-Waitt), and B. O'Bannon (RJE) for logistical support. S. Kawatsu, T. Narazaki, and K. Q.

Sakamoto gave helpful advice on data analysis and R. Hueter, A. Gleiss, and 3 anonymous reviewers provided useful comments on the manuscript. J. Castro provided shark profile drawings for Figs. 1 & 4. This study was funded by the Waitt Institute for Discovery, the National Geographic Society, and the National Shark Research Consortium (NOAA). D. Vaughan provided valuable equipment and support to H.L.P.

LITERATURE CITED

➤ Carrier JC, Pratt HL (1998) Habitat management and closure of a nurse shark breeding and nursery ground. Fish Res 39:209–213

➤ Carrier JC, Pratt HL Jr, Martin LK (1994) Group reproductive behaviour in free-living nurse sharks, *Ginglymostoma cirratum*. Copeia 1994:646–656

Carrier JC, Pratt HL Jr, Castro JI (2004) Reproductive biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives, Vol 10. CRC Press, Boca Raton, FL, p 269–286

➤ Chapman DD, Prodohl PA, Gelsleichter CA, Manire CA, Shivji MS (2004) Predominance of genetic monogamy by females in a hammerhead shark, *Sphyrna tiburo*: implications for shark conservation. Mol Ecol 13:1965–1974

Cornish AS (2005) First observation of mating in the bamboo shark *Hemiscyllium freycineti* (Chondrichthyes: Hemiscylliidae). Zool Stud 44:454–457

Cortés E, Brooks L, Scott G (2002) Stock assessment of large coastal sharks in the US Atlantic and Gulf of Mexico. Sustainable Fisheries Division Contribution SFD-2/03-177, National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City, FL

➤ Daly-Engel TS, Grubbs RD, Bowen BW, Toonen RJ (2007) Frequency of multiple paternity in an unexploited tropical population of sandbar sharks (*Carcharhinus plumbeus*). Can J Fish Aquat Sci 64:198–204

➤ DiBattista JD, Feldheim KA, Gruber SH, Hendry AP (2008) Are indirect genetic benefits associated with polyandry? Testing predictions in a natural population of lemon sharks. Mol Ecol 17:783–795

➤ Feldheim KA, Gruber SH, Ashley MV (2004) Reconstruction of parental microsatellite genotypes reveals female polyandry and philopatry in the lemon shark, *Negaprion brevirostris*. Evolution 58:2332–2342

Francis MP (1996) Observations on a pregnant white shark with a review of reproductive biology. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharadon carcharias*. Academic Press, San Diego, CA, p 157–172

Gleiss AC, Gruber SH, Wilson RP (2009a) Multi-channel data-logging: towards determination of behaviour and metabolic rate in free-swimming sharks. In: Nielsen JL, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, Sibert J (eds) Tagging and tracking of marine animals with electronic devices. Springer, Dordrecht, p 211–228

➤ Gleiss AC, Norman B, Liebsch N, Francis C, Wilson RP (2009b) A new prospect for tagging large free-swimming sharks with motion-sensitive data-loggers. Fish Res 97: 11–16

Halsey LG, Shepard ELC, Quintana F, Gomez Laich A, Green JA, Wilson RP (2009) The relationship between oxygen consumption and body acceleration in a range of species. Comp Biochem Physiol A 152:197–202

➤ Harvey-Clark CJ, Stobo WT, Helle E, Mattson M (1999) Putative mating behaviour in basking sharks off the Nova Scotia coast. Copeia 1999:780–782

Hoenig JM, Gruber SH (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources. NOAA Tech Rep NMFS 90:1–16

➤ Kato A, Ropert-Coudert Y, Grémillet D, Cannell B (2006) Locomotion and foraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. Mar Ecol Prog Ser 308:293–301

➤ Kawabe R, Nashimoto K, Hiraishi T, Naito Y, Sato K (2003) A new device for monitoring the activity of freely swimming flatfish, Japanese flounder, *Paralichthys olivaceus*. Fish Sci 69:3–10

➤ Lagarde F, Guillon M, Dubroca L, Bonnet X, Ben Kaddour K, Slimani T, El mouden EH (2008) Slowness and acceleration: a new method to quantify the activity budget of chelonians. Anim Behav 75:319–329

➤ Marshall G, Bakhtiari M, Shepard M, Tweedy J III and others (2007) An advanced solid-state animal-borne video and environmental data-logging device (Crittercam) for marine research. Mar Technol Soc J 41:31–38

McCauley DJ, Papastamatiou YP, Young HS (in press) Mating behavior in free-ranging blacktip reef sharks, *Carcharhinus melanopterus*. Pac Sci

Metcalfe JD, Fulcher MC, Clarke SR, Challiss MJ, Hetherington S (2009) An archival tag for monitoring key behaviours (feeding and spawning) in fish. In: Nielsen JL, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, Sibert J (eds) Tagging and tracking of marine animals with electronic devices. Springer, Dordrecht, p 243–254

Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S (2000) Management of sharks and their relatives (Elasmobranchii). Fisheries 25:9–13

➤ Papastamatiou YP, Meyer CG, Holland KN (2007) A new acoustic pH transmitter for studying the feeding habits of free-ranging sharks. Aquat Living Resour 20:287–290

➤ Portnoy DS, Piercy AN, Musick JA, Burgess GH, Graves JE (2007) Genetic polyandry and sexual conflict in the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic and Gulf of Mexico. Mol Ecol 16:187–197

➤ Powter DM, Gladstone W (2008) The reproductive biology and ecology of the Port Jackson shark *Heterodontus portusjacksoni* in the coastal waters of eastern Australia. J Fish Biol 72:2615–2633

➤ Pratt HL Jr, Carrier JC (2001) A review of elasmobranch reproductive behaviour with a case study on the nurse shark, *Ginglymostoma cirratum*. Environ Biol Fishes 60:157–188

Pratt HL Jr, Carrier JC (2005) Elasmobranch courtship and mating behaviour. In: Hamlett WC (ed) Reproductive behaviour and phylogeny of elasmobranchs, Vol 3. Science Publishers, Enfield, NH, p 129–169

Pratt HL Jr, Carrier JC (2007) The nurse shark: mating and nursery habitat in the Dry Tortugas, Florida. In: McCandless C, Kohler NE, Pratt HL Jr (eds) Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States. American Fisheries Society, Baltimore, MD, p 225–236

Pratt HL Jr, Casey JG (1990) Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth parameters. In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources. NOAA Tech Rep NMFS 90: 97–110

Rasmussen LEL, Hess DL, Gruber SH (1992) Serum steroid hormones during reproduction in elasmobranchs. In: Hamlett WC (ed) Reproductive biology of South American vertebrates. Springer-Verlag, New York, p 19–42

Rowe S, Hutchings JA (2003) Mating systems and the conservation of commercially exploited marine fish. Trends Ecol Evol 18:567–572

Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? PLoS ONE 4:e5379

Sato K, Sakamoto KQ, Watanuki Y, Takahashi A, Katsumata N, Bost CA, Weimerskirch H (2009) Scaling of soaring seabirds and implications for flight abilities of giant pterosaurs. PLoS ONE 4:e5400

Saville KJ, Lindley AM, Maries EG, Carrier JC, Pratt HL Jr (2002) Multiple paternity in the nurse shark (*Ginglymostoma cirratum*). Environ Biol Fishes 63:347–351

Shepard ELC, Wilson RP, Quintana F, Laich AG and others (2008) Identification of animal movement patterns using tri-axial accelerometry. Endang Species Res doi:10.3354/esr00084

Smith SE (2005) Leopard shark mating observed off La Jolla, California. Calif Fish Game 91:128–135

Springer S (1967) Social organization of shark populations. In: Gilbert PW, Mathewson RF, Rall DP (eds) Sharks, skates, and rays. Johns Hopkins Press, Baltimore, MD

Tanaka H, Takagi Y, Naito Y (2001) Swimming speeds and buoyancy compensation of migrating adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger. J Exp Biol 204:3895–3904

Tricas TC, LeFeuvre EM (1985) Mating in the reef white-tip shark, *Triaenodon obesus*. Mar Biol 84:233–237

Tsuda Y, Kawabe R, Tanaka H, Mitsunaga Y, Hiraishi T, Yamamoto K, Nashimoto K (2006) Monitoring the spawning behaviour of chum salmon with an acceleration data logger. Ecol Freshw Fish 15:264–274

Watanabe S, Izawa M, Kato A, Ropert-Coudert Y, Naito Y (2005) A new technique for monitoring the detailed behaviour of terrestrial animals: a case study with the domestic cat. Appl Anim Behav Sci 94:117–131

Watanabe Y, Wei Q, Yang D, Chen X and others (2008) Swimming behaviour in relation to buoyancy in an open swim-bladder fish, the Chinese sturgeon. J Zool 275:381–390

Watanuki Y, Niizuma Y, Gabrielsen GW, Sato K, Naito Y (2003) Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. Proc R Soc B 270:483

Watanuki Y, Takahashi A, Daunt F, Wanless S, Harris M, Sato K, Naito Y (2005) Regulation of stroke and glide in a foot-propelled avian diver. J Exp Biol 208:2207–2216

Whitney NM, Pratt HLJ, Carrier JC (2004) Group courtship, mating behaviour, and siphon sac function in the whitetip reef shark, *Triaenodon obesus*. Anim Behav 68:1435–1442

Whitney NM, Papastamatiou YP, Holland KN, Lowe CG (2007) Use of an acceleration data logger to measure diel activity patterns in captive whitetip reef sharks, *Triaenodon obesus*. Aquat Living Resour 20:299–305

Wilson RP, Scolaro A, Quintana F, Siebert U and others (2004) To the bottom of the heart: cloacal movement as an index of cardiac frequency, respiration and digestive evacuation in penguins. Mar Biol 144:813–827

Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. J Anim Ecol 75: 1081–1090

Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. Endang Species Res 4:123–137

Yoda K, Sato K, Niizuma Y, Kurita M, Bost CA, Le Maho Y, Naito Y (1999) Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. J Exp Biol 202:3121–3126

Editorial responsibility: Rory Wilson,
Swansea, UK

Submitted: May 21, 2009; Accepted: October 21, 2009
Proofs received from author(s): January 19, 2010