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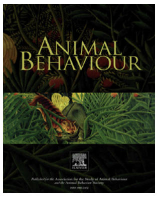

Short-term impacts of daily feeding on the residency, distribution and energy expenditure of sharks

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Tourism-related feeding of wildlife can result in detrimental, human-induced changes to the spatial distribution, social behaviour and health of target species. The feeding of sharks as part of shark-viewing activities has become increasingly popular in recent years to ensure reliable and consistent encounters. A common limitation in determining how feeding affects individuals or populations is the lack of baseline data prior to the establishment of a feeding site. Here, we documented the residency, spatial distribution, activity patterns and daily metabolic rates of juvenile lemon sharks, *Negaprion brevirostris*, prior to initiating daily feeding for 27 days to assess the effect of short-term feeding. We implanted acoustic transmitters equipped with accelerometers to record movement and activity in six lemon sharks. Sharks progressively anticipated the feeding events during the 27 days of daily feeding, as shown by a change in activity and increased time spent near the feeding site 1 h prior to feeding events. Shark behaviour did not fully return to baseline levels within the documented 90 days of postfeeding recovery. However, neither spatial distribution outside the refuge nor mean daily activity was affected by feeding. Sharks decreased their metabolic rates over the course of the study, but this was probably due to falling water temperature rather than the effect of feeding. Overall, our study shows that anticipatory behaviour in juvenile lemon sharks can occur within 11 days of daily feeding events, but behavioural changes seem confined to fine-scale movement patterns and may not affect these sharks' daily energy needs. The ability to assess the effects of daily feeding at a site where tourism has not been occurring previously provides new information for operators and managers of wildlife tourism to account for and minimize potentially detrimental effects on the target species.

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In recent decades, wildlife tourism has become one of the fastest-growing sectors of the tourism industry (Scheyvens, 1999; Wearing & Neil, 2009), partly due to the increasing desire of people to reconnect with nature (Miller, 2005). Associated with a number of socioeconomic benefits (Apps, Dimmock, & Huveneers, 2018; Huveneers et al., 2017; Newsome, Rodger, Pearce, & Chan, 2019; Orams, 2002), wildlife tourism has been viewed as a tool to assist local economies transitioning from consumptive to perceived nonconsumptive uses of natural resources (Newsome et al., 2019). To name just a few, examples include lemur- and birdwatching tourism in Andasebe National Park (Newsome & Hassell, 2014), gorilla and chimpanzee tourism in Uganda (Newsome & Hughes, 2016), whale-watching tourism in the Antarctic (Williams & Crosbie, 2007), and shark and ray tourism in the Bahamas and Fiji (Haas, Fedler, & Brooks, 2017; Macdonald et al., 2017). These examples illustrate how the employment of local tour guides and the provision of other services by local communities can result in economic success and growth (Newsome et al., 2019). Linked with an increased public awareness for endangered species, these economic transitions can also benefit the focal species and their surrounding ecosystems by promoting conservation efforts (Apps

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et al., 2018; Newsome & Hassell, 2014). However, previous studies have indicated detrimental effects of wildlife tourism activities (Barnett, Payne, Semmens, & Fitzpatrick, 2016; Green & Giese, 2004; Newsome, Lewis, & Moncrieff, 2004; Semeniuk & Rothley, 2008), and the resulting impaired individual fitness and survival has been documented in terrestrial (Orams, 2002), avian (Steven, Pickering, & Castley, 2011) and aquatic species (Williams & Crosbie, 2007). For example, close proximity and interactions of tourists with Adélie penguins, *Pygoscelis adeliae*, has resulted in as much as an 80% reduction in chick survival (Giese, 1996). Behavioural changes due to wildlife tourism can also lead to decreased survival, such as with coastal damselfish, *Chromis chromis* (Milazzo, Anastasi, & Willis, 2006), or can increase aggressive behaviours towards humans, such as with yellow baboons, *Papio cynocephalus*, in Kenya and dingoes, *Canis lupus dingo*, on Fraser Island, Australia (Altmann & Muruthi, 1988; Burns & Howard, 2003).

Recent studies on elasmobranchs have shown that wildlife tourism can have a wide range of effects on focal and nonfocal species, including changes in seasonality, residency, abundance (Clarke, Lea, & Ormond, 2011; Meyer, Dale, Papastamatiou, Whitney, & Holland, 2009), space use (Bruce & Bradford, 2013; Brunnschweiler & Barnett, 2013; Fitzpatrick, Abrantes, Seymour, & Barnett, 2011; Huveneers et al., 2013), activity (Corcoran et al., 2013; Huveneers, Watanabe, Payne, & Semmens, 2018) and diet (Brunnschweiler, Payne, & Barnett, 2018; Meyer, Whitmarsh, Nichols, Revill, & Huveneers, 2020). Such effects are often accentuated by feeding the focal species to ensure reliable and close encounters (Brena, Mourier, Planes, & Clua, 2015; Gallagher et al., 2015). For instance, Brunnschweiler and Barnett (2013) demonstrated changes in the fine-scale movement patterns of bull sharks, *Carcharhinus leucas*, that are frequently exposed to wildlife feeding operations in Fiji. They further found evidence suggesting significant intraspecific variation with regard to the effects of wildlife feeding (Brunnschweiler & Barnett, 2013). Besides the growing body of knowledge on the effects of feeding activities on the behaviours of elasmobranch species, few studies have investigated tourism-related changes in energy expenditure of sharks (e.g. Barnett et al., 2016; Huveneers et al., 2018). This information is, however, crucial to understand the effects of wildlife tourism (Brown, Gillooly, Allen, Savage, & West, 2004; Brunnschweiler et al., 2018; Gallagher & Huveneers, 2018; Wilson et al., 2006). A study on whitetip reef sharks, *Triaenodon obesus*, at Osprey Reef (Great Barrier Reef, Australia) demonstrated that sharks subjected to regular feeding events showed elevated activity levels during the day when they would normally rest, resulting in a ca. 6.4% increase in metabolic rates. Similarly, white sharks, *Carcharodon carcharias*, are more active when interacting with cage-diving operators (Huveneers et al., 2018).

A common limitation in studies investigating the effects of direct feeding (hereafter referred to as ‘feeding’) is the lack of baseline data prior to establishing a feeding site (Huveneers et al., 2013; Semeniuk & Rothley, 2008). While a population that is not being fed can act as a control, observed differences can be due to site-specific factors. Instead, a more reliable approach for assessing the effects of feeding is one where baseline data can be collected prior to initiation of wildlife tourism activities. If feeding activities can occur for a finite period of time, it further provides the opportunity to investigate behaviour after they stop to assess how soon behaviours return to baseline levels. Therefore, gaining an understanding of a target species' behavioural ecology prior to the establishment of a new feeding site will help wildlife tourism managers to implement sustainable strategies, minimizing the negative impacts of these activities. Ultimately, this will provide further insight about the timing, location and frequency of feeding activities, as well as limits on the number of boats and people allowed to participate, similar to some of the guidelines developed for the whale-watching industry (Mallard, 2019).

Here, we first established a feeding site in Bimini (Bahamas), targeting juvenile lemon sharks, *Negaprion brevirostris*, in a known nursery area where wildlife tourism has not occurred (Guttridge et al., 2012). We used acoustic telemetry and accelerometry to assess daily activity, metabolic rates and spatial distribution patterns before, during and after a 1-month (daily) feeding regime. The aim of this study was to investigate whether daily feeding of juvenile lemon sharks at an aggregation site (1) resulted in anticipatory behaviour, as measured by changes in burst activity and fine-scale distribution, (2) increased activity, thereby affecting metabolic rate, and (3) affected the sharks’ spatial distribution. We hypothesized that daily feeding would (1) lead to sharks anticipating feeding events, (2) increase daily activity and metabolic rates and (3) constrict space use of juvenile lemon sharks.

METHODS

Study Site and Species

The study was conducted in Bimini (25°44′N, 79°16′W), Bahamas (island group located ca. 90 km east of Florida, U.S.A.; Fig. 1) at a tidally mediated refuge site for juvenile lemon sharks known locally as ‘Aya's Spot’. The area (ca. 200 m long and 20 m wide) is a shallow water mangrove inlet that becomes inaccessible during low tides and provides protection from predators over the high tides due to the narrow (<1 m), shallow entrance (Guttridge et al., 2012). Juvenile lemon sharks use the area daily, with 7 ± 4 (mean ± SD) sharks aggregating in the northern part of the refuge at and around the high tide (Guttridge, Gruber, Krause, & Sims, 2010; Guttridge et al., 2011).

Acoustic Monitoring

Ten acoustic receivers (model VR2W–69Hz, Vemco, Halifax, Nova Scotia) were deployed in a nonoverlapping array within 2.5 km of Aya's Spot (Fig. 1). One receiver was positioned at the single access point of Aya's Spot (refuge entrance), providing acoustic coverage of sharks entering or departing. Receivers were deployed inside a PVC housing with a concrete base (see Guttridge et al. (2012) for more details on the housing). Range testing using three stationary transmitters and two receivers placed at <1 m depth in a similar habitat to the present study showed a detection range of 50–100 m, depending on the tidal phase (Guttridge et al., 2017; Murchie et al., 2010). This range is relatively small compared to the range of receivers in open environments (Huveneers et al., 2016) and probably due to the shallow habitat. Temperature loggers (HOBO Water Temperature Pro v2 Data Logger, Onset Computer Corporation, Bourne, MA, U.S.A.) were placed at four of the 10 receivers (Fig. 1), which recorded the ambient water temperature at 30 min intervals. In addition to the 10 receivers placed around Aya's Spot, 55 receivers had already been deployed around Bimini (Fig. 1) as part of a long-term acoustic monitoring project (Guttridge et al., 2017).

Juvenile lemon sharks were trapped using two seine nets (10 cm monofilament stretch mesh) that closed off Aya's Spot during the last hour of the rising tide. Juvenile lemon sharks were caught individually using dip nets as they attempted to leave Aya's Spot during the falling tide. Each shark was processed immediately upon capture and released before the next individual was caught. Upon capture, individual sharks were immediately transferred into a 200-litre tank where precaudal length was measured to the nearest millimetre and sex was determined (Dhellemmes, Finger, Laskowski, Guttridge, & Krause, 2020). Nine sharks (five females

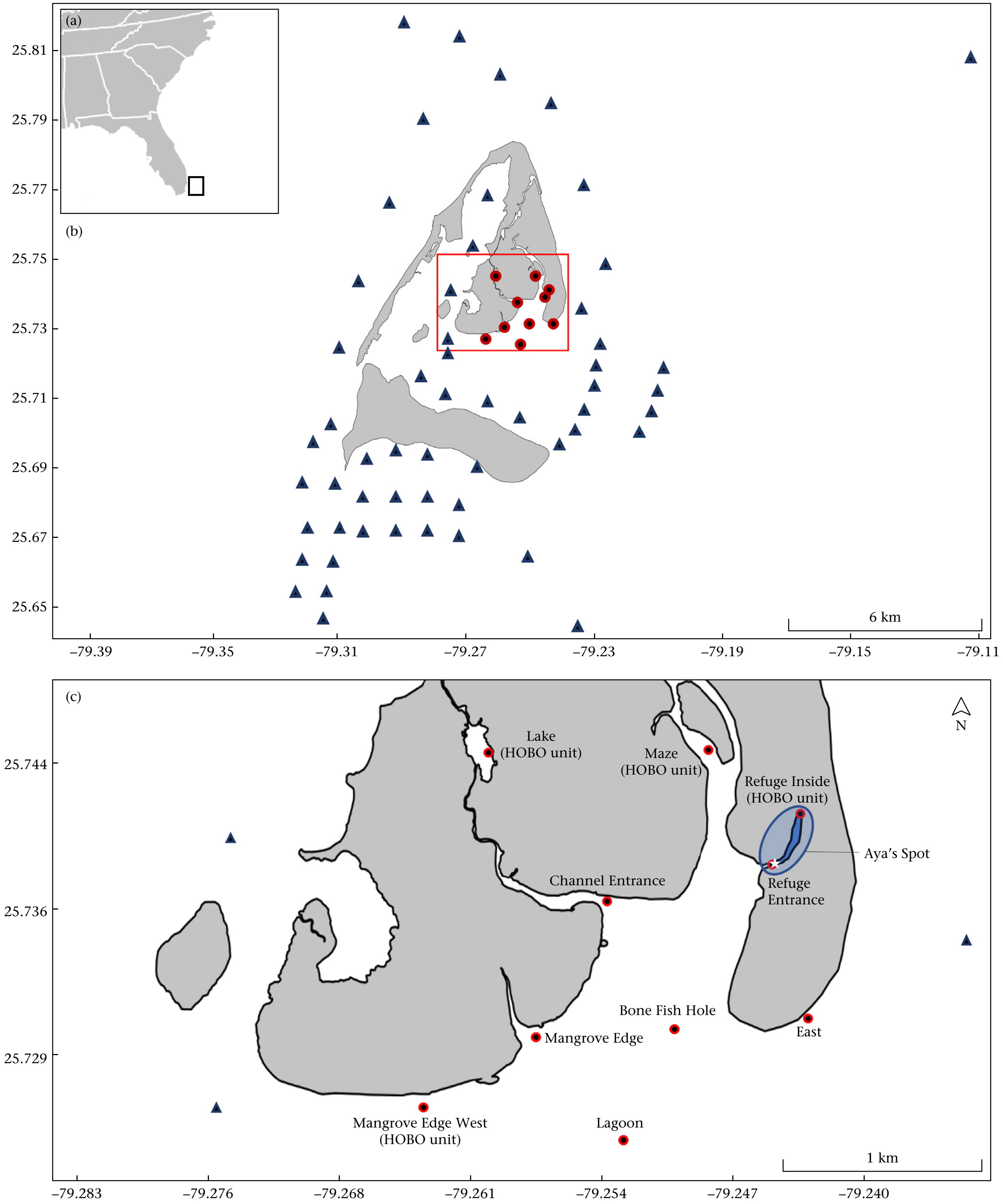

Figure 1. Maps of the study site showing (a) the position of the Bimini island group relative to Florida, U.S.A. and (b) an overview of the Bimini island group and the distribution of VR2W acoustic receivers around Bimini. Each marker represents one receiver. Blue triangles mark the locations of the receivers that are part of a long-term acoustic monitoring project. Red dots mark the receivers that were deployed for this study. (c) Map of the study site and the Aya's Spot refuge (blue polygon). Locations of HOBO water temperature loggers are also indicated as 'HOBO unit' underneath each receiver name. The white star next to the Refuge Entrance receiver marks the feeding site.

and four males, between 1 and 3 years old) were equipped with an acoustic activity tag (V13AP, Vemco, Halifax, Nova Scotia) that was surgically implanted into the peritoneal cavity through a small (30–40 mm) incision along the ventral side of the shark. The incision was closed with interrupted absorbable sutures (Ethicon braided coated Vicryl) that were tied using a surgeon's knot (Wagner, Stevens, & Byrne, 2000). All procedures combined took less than 8 min per individual with the surgery being completed while sharks were held by hand in tonic immobility (Kessel & Hussey, 2015). This is a coma-like state that is achieved by turning sharks quickly on their backs. One member of the research team handheld the shark in this position, while another performed the surgical implantation. It is widely recognized as an effective alternative to chemical anaesthetics, providing several benefits, both from a practical and an animal welfare perspective (reviewed in Kessel & Hussey, 2015). Besides a rapid induction and recovery, which optimizes the surgical procedure, there is no risk of overdose and minimal disruption to respiration, thereby reducing the risk for negative sublethal impacts (Kessel & Hussey, 2015). Each shark was further marked with a unique second, external tag (colour coded T-bar tag; Floy Tag Manufacturing, Seattle, WA, U.S.A.) through the first or second dorsal fin. Following processing, all nine sharks swam away vigorously and were later detected via acoustic receivers or visual observations, thereby confirming survival.

Acceleration and depth data were transmitted at random intervals of 120–180 s. Acceleration (±4.9 m/s^2 range) was sampled at 5 Hz for 20 s four times every five transmission cycles (10–15 min). Activity was calculated as an average root mean square (RMS) value for all three axes ($\text{activity} = [X^2 + Y^2 + Z^2]^{0.5}$) and transmitted as an 8-bit digital value. The static contribution to the overall acceleration (g) was filtered out prior to RMS calculation. RMS acceleration resolution was 0.0191 m/s^2 (Payne et al., 2011).

Experimental Protocol

Sharks were given 10 days to recover from capture-associated stress (Bullock, Guttridge, Cowx, Elliott, & Gruber, 2015) and surgery (Chin, Mourier, & Rummer, 2015). Following this recovery period, they were not disturbed for an additional 30 days, which provided time to record natural behaviours. Sharks were then attracted to the feeding site using a bait box filled with fish scraps and target-fed daily for 27 days using feeding poles to ensure minimal physical interactions between the feeders and the sharks. We ensured each shark received the same amount of food, approaching their estimated daily ration in the wild (i.e. up to 2% of their body mass; Sims, 1996). This amount was chosen based on learning trials on captive juvenile lemon sharks where feeding motivation was maintained across several months (Guttridge et al., 2013). Each day, the feeding event commenced 1 h before the daytime high tide. This schedule was used because juvenile lemon sharks in this area were already known to use Aya's Spot as a refuge during this time (Guttridge et al., 2012). The feeding area at Aya's Spot was marked with three vertical PVC pipes that were painted with black and white stripes and anchored to the substrate using steel bars. The PVC pipes acted as landmarks to help sharks learn to associate the tide cycle and the feeding event. Black and white panels have been used previously to demonstrate social learning in juvenile lemon sharks in Bimini (Guttridge et al., 2013). Feeding duration was 1 h until the peak high tide was reached. For each feeding event we recorded time of first arrival for each individual, as well as the maximum number of sharks that arrived. We were unable to feed on four occasions due to inclement weather (days 15, 23, 24 and 26). Sharks were no longer fed after the 27-day period, but acoustic receivers remained deployed for an additional 90 days to record changes in behaviour once the daily feeding events had ceased.

Data Analyses

Anticipation

Anticipatory behaviour was investigated using the proportion of high-activity events (Burst Activity; >0.9 m/s^2) across feeding times (1 h before [prefeeding], during [feeding] and 1 h after [postfeeding]). We expected that anticipation would lead to increased Burst Activity during prefeeding. We selected the threshold of 0.9 m/s^2 to represent periods of elevated activity that appeared to be associated with the feeding events based on the frequency distribution of activity measurements and the prominent shift of the distribution towards higher levels of activity during the feeding period (Fig. A1). We also evaluated whether anticipatory behaviour was occurring by assessing the proportion of detections around the daytime high tides at the refuge entrance receiver located next to the feeding site (Spatial Attraction). The proportion was obtained by dividing the number of detections at the refuge entrance receiver by the total number of detections from both Aya's Spot refuge receivers. We used Spatial Attraction as a measure of anticipation, since previous observations showed that sharks spend most of their time inside Aya's Spot during high tide (Guttridge et al., 2012). An increase in Spatial Attraction would indicate that the sharks moved closer to the feeding site in anticipation of the upcoming feeding event. This enabled us to determine how much time sharks were spending in proximity to the feeding site. Spatial Attraction was compared across feeding times. To investigate the point in time when the sharks started to anticipate the feedings, we visually compared the time of first arrival and the maximum number of sharks present during the feeding events across days. We defined a learning criterion to identify the approximate time it took for sharks to start anticipating the feeding events. A shark had reached the criterion once it arrived at the feeding site within 6 min after the beginning of the feeding event on 3 consecutive days. We also extended the recovery period to 90 days to determine when the anticipatory behaviour ceased. The 90-day recovery period was split into three subperiods of 30 days called recovery 30, recovery 60 and recovery 90, respectively.

Daily activity and metabolic rates

We investigated whether daily feeding events affected mean activity (obtained from the activity tag) and metabolic rate. Given that the formula used to calculated metabolic rate ($\dot{M}_{O_2}$) requires the overall dynamic body acceleration (ODBA) in g ($1\ g = 9.80665\ m/s^2$), we first converted the activity tag values by dividing them by the Earth's gravitational pull (9.81 m/s^2). Metabolic rate ($\dot{M}_{O_2}$) was estimated following Lear et al. (2017):

$$\dot{M}_{O_2} = \alpha(\text{ODBA}) + b, \tag{1}$$

where α is the slope and b the intercept of the ODBA–$\dot{M}_{O_2}$ relationship. While being species specific, α remains independent of environmental influences. The intercept b, however, varies with environmental factors, in our case water temperature, which scales the intercept as follows:

$$b = b_c \times S^{\frac{T_b - T_c}{10}}, \tag{2}$$

where T_b is the temperature at which the intercept b is calculated. The intercept of the ODBA–$\dot{M}_{O_2}$ relationship b_c is the intercept that was assessed during the calibration at temperature T_c. S is the scaling factor that was determined for the species, also known as the Q_{10}. All constant variables (α, b_c, T_c and S) were obtained from

Lear et al. (2017), who calibrated the ODBA–$\dot{M}_{O_2}$ relationship at two different temperatures in three different species of sharks, including lemon sharks. Water temperatures were calculated as the mean temperatures from four temperature loggers (HOBO Water Temperature Pro v2 Data Logger, Onset Computer Corporation) deployed at the study site (Fig. 1).

Spatial distribution

For our assessment of the spatial distribution of juvenile lemon sharks across the five periods (baseline, feeding, recovery 30, recovery 60 and recovery 90), we assumed that the detection efficiency was homogeneous across the receivers deployed in the study, which was reasonable, given the identical depth and habitat type. We used the packages VTrack (Campbell, Watts, & Dwyer, 2012) and Animal Tracking Toolbox (Udyawer et al., 2018) in R v.4.0.0 (R Core Team, 2013) to create Brownian Bridge kernel utilization density models (BB-KUD) based on all detections recorded during each of the five periods. These models account for the movement paths between two fixed locations when calculating the movement range of an animal, using random walks between two successive locations based on the distance between the locations and the time it took an animal to cover this distance (Fischer, Walter, & Avery, 2013; Horne, Garton, Krone, & Lewis, 2007). Calculating the BB-KUDs enabled us to quantitatively compare the activity space of the sharks and to statistically assess whether the daily feedings significantly affected said activity space (Fischer et al., 2013; Udyawer et al., 2018). We calculated the 50% (BB-KUD50 or core area hereafter) and 95% (BB-KUD95 or home range hereafter) ranges of the BB-KUDs and compared them statistically using a linear mixed model (LMM). Visualizing the extents of the BB-KUDs, we further investigated whether the core area shifted between periods.

In summary, we used five response variables to assess the effects of daily feeding events on shark behaviour: (1) Burst Activity, (2) Spatial Attraction, (3) daily activity, (4) daily metabolic rates, and (5) core area and home range. Burst Activity and Spatial Attraction were estimated for each prefeeding, feeding and postfeeding event; daily activity and daily metabolic rates were estimated for each day of the study; core area and home range were estimated for each period (data were collected (24 h a day) calculated for the baseline, feeding and three recovery periods). As feeding events only occurred during the day, the analyses of anticipatory behaviours (i.e. Burst Activity and Spatial Attraction) were restricted to daytime high tides. Night-time behaviour was also assessed and is presented in the Appendix.

Generalized linear mixed models (GLMMs) were used with Period (baseline, feeding, recovery 30, recovery 60, recovery 90) as a fixed factor; Time (prefeeding, feeding, postfeeding; fixed factor) was also included in the models assessing anticipatory behaviour (Fig. A2). We further included Temperature (continuous, fixed factor) for the analyses of mean daily activity and metabolic rates because of its known impact on metabolic rates (Lear et al., 2017). Day and Shark ID were included as random factors in all GLMMs to account for the lack of independence in the behaviour of each shark and across days. We included a random slope grouped by Shark ID in the GLMM assessing the effects of feeding on the daily activity measurements. For the remaining models we were unable to include a random slope due to convergence issues. The error structure of GLMM corrects for nonindependence of statistical units due to shared temporal structure (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We determined the most appropriate statistical family and error distribution for each analysis by examining the distribution of the response variables and visually inspecting the residuals for the saturated models in accordance with Zuur, Ieno, and Elphick (2010). Data transformations were used where appropriate to improve model fit as follows: (1) Burst Activity and Spatial Attraction models: binomial (logit) distribution, no transformations; (2) daily activity and metabolic rate models: Gaussian (identity) distribution with Box–Cox transformations. For the comparison of the BB-KUD ranges between periods, we used an LMM with a restricted maximum likelihood fit, no transformations, and Shark ID as a random factor. We used a dredge function from the R package MuMIn (Barton, 2019) to identify more parsimonious nested models based on their relative probabilities using Akaike's information criterion corrected for small sample size (AIC_c; Burnham, Anderson, & Huyvaert, 2011). We used the AIC_c weights ($wAIC_c$) of all the potential models to calculate the relative variable importance values (RVI) to assess the impact of each variable on the statistical outcome. For all models we took a two-tailed approach, accepting significant results regardless of the direction of change. We used post hoc Tukey tests to test for statistical differences between periods. We did not run post hoc Tukey tests on the model outcomes investigating the daily activity and the metabolic rates due to the interaction between a categorical (Period) and a continuous (Temperature) variable. All analyses were performed in R v.4.0.0 (R Core Team, 2013) using the packages glmmTMB (Brooks et al., 2017) and lsmeans (Lenth, 2016). Graphs were created in R v.4.0.0 (R Core Team, 2013) using the packages ggplot2 (Wickham, 2016) and plotly (Sievert et al., 2017).

Ethical Note

The research was approved by the Flinders University Animal Welfare Committee (E452/17) and by the Ministry of Agriculture and Marine Resources, Nassau, Bahamas (Marine Scientific Research Permit).

The sample size was reduced as much as possible, while still ensuring meaningful results (Sequeira et al., 2019). All handling, including the capture of the sharks with dip nets, was done as quickly as possible to minimize stress. Sharks were caught individually and immediately processed and released. As a result, no shark was confined and handled for more than 8 min.

RESULTS

Of the nine juvenile lemon sharks tagged, two were only detected for 9 days post tagging and not during the feeding or recovery periods. Therefore, we omitted these two individuals from further analyses. The remaining seven sharks were regularly detected at Aya's Spot until the end of the study on 13 January 2018. We documented 4530 ± 650 detections per shark with ca. 94% of these occurring at the two Aya's Spot receivers. None of the tagged sharks were detected on receivers outside the 10 receivers deployed for this project (Fig. 1). Of the seven sharks successfully tracked, six frequently participated in the feeding events. The seventh shark was frequently detected on Aya's Spot receivers but did not participate in the feeding events and was therefore omitted from the analyses. Between the tagged and untagged sharks that frequented Aya's Spot, on average 7 ± 2 participated in the feedings. Based on personal observations we made during this study (maximum number of sharks observed inside Aya's spot was 11) and the maximum daily number of sharks that was reported by Guttridge et al. (2012) to visit Aya's Spot, we estimate that 70–90% of the sharks that frequented Aya's Spot during the time of our experiment participated in the feeding events.

Anticipation: Prefeeding Burst Activity and Spatial Attraction

Burst Activity was affected by the interaction between Period and Time ($wAIC_c = 1.00$; Table 1, Appendix Table A1). It increased significantly during the 1 h leading up to the feeding events (post hoc Tukey: $\beta = -0.909$, $t_{9223} = -3.806$, $P = 0.012$) but dropped back to baseline levels within the first 30 days of recovery (post hoc Tukey: recovery 30: $\beta = 0.126$, $t_{9223} = 0.495$, $P = 1.000$; Fig. 2, Table 1). At night, there were no signs of anticipation based on Burst Activity (Appendix Tables A2, A3, Fig. A3).

Spatial Attraction was also affected by the interaction between Period and Time ($wAIC_c = 1.00$; Table 1, Appendix Table A1). It increased for the 1 h of prefeeding during the feeding month (post hoc Tukey: $\beta = -5.568$, $t_{11447} = -5.003$, $P = 0.0001$; Fig. 2) and remained significantly higher during the 1 h of prefeeding throughout the 90 days of recovery compared to the baseline period (post hoc Tukey: recovery 30: $\beta = -7.440$, $t_{11447} = -6.746$, $P < 0.0001$; recovery 60: $\beta = -8.000$, $t_{11447} = -7.342$, $P < 0.0001$; recovery 90: $\beta = -3.885$, $t_{11447} = -3.477$, $P = 0.038$; Fig. 2). However, prefeeding Spatial Attraction started to decrease during recovery 90 and was significantly lower compared to recovery 60 (post hoc Tukey: $\beta = 4.115$, $t_{11447} = 4.033$, $P = 0.005$). During the 1 h of postfeeding, Spatial Attraction was significantly higher during the feeding month (post hoc Tukey: $\beta = -11.257$, $t_{11447} = -7.467$, $P < 0.0001$; Fig. 2). Despite an initial drop during the first 30 days of recovery, the postfeeding Spatial Attraction remained significantly higher than the baseline level during recovery 60 (post hoc Tukey: $\beta = -5.602$, $t_{11447} = -4.520$, $P = 0.0006$; Fig. 2).

Spatial learning and anticipation appear to have commenced after 9 days. This estimate is based on the number of sharks observed during the feeding events and the significant drop in latencies to first arrival (linear regression: Latency to first arrival ~ Day: $\beta = -0.637$, $t_{119} = -4.215$, $P < 0.0001$; Fig. 3). Five of the six sharks included in the analysis reached the learning criterion and did so in 10.8 ± 0.37 days (Fig. 3). In contrast to Burst Activity, the Spatial Attraction 1 h prior to the feeding events started to increase significantly during night-time high tides (slack tide was reached between sunset and 1 h after sunrise) during the feeding period and was retained for the first 60 days of recovery (Appendix Tables A2, A3, Fig. A3).

Daily Activity (Overall Dynamic Body Acceleration) and Metabolic Rates

Daily overall dynamic body acceleration was significantly affected by the interaction between Period and Temperature ($wAIC_c = 1.00$; Table 2, Appendix Table A4). Although it increased with temperature during the baseline and feeding months, the slope was very small (Fig. 4, Table 2). It remained consistent during

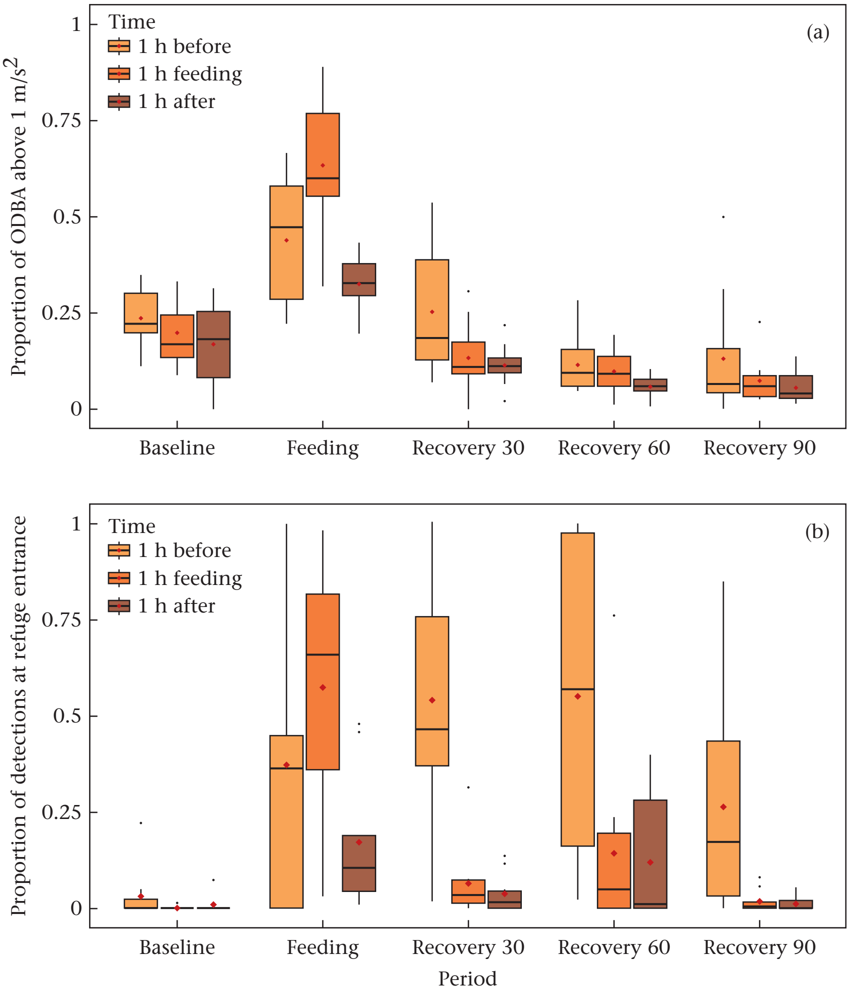

Figure 2. Box plot illustrating (a) the proportion of overall dynamic body acceleration (ODBA, m/s^2) above 0.9 m/s^2 (Burst Activity), and (b) the proportion of detections made at the refuge entrance (number of detections at refuge entrance/(number of detections at refuge entrance + number of detections inside refuge)) (Spatial Attraction) plotted against the Period. The horizontal lines inside the boxes mark the median and the red diamonds the mean for 1 h before, during and after feeding events. The upper and lower boundaries of the box represent the third and first quartiles. The whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

Table 1
Summary table for the models investigating the Period and Time effects on Burst Activity and Spatial Attraction

Effect	β	SE	z	P
Burst Activity				
(Intercept)	−1.390	0.235	−5.920	<0.001
Period (feeding)	0.885	0.245	3.609	<0.001
Period (recovery 30)	−0.166	0.264	−0.630	0.529
Period (recovery 60)	−0.888	0.241	−3.684	<0.001
Period (recovery 90)	−1.010	0.276	−3.661	<0.001
Time (during)	0.051	0.164	0.309	0.757
Time (after)	0.056	0.176	0.318	0.750
Period (feeding) * Time (during)	0.873	0.238	3.663	<0.001
Period (recovery 30) * Time (during)	−0.429	0.277	−1.549	0.121
Period (recovery 60) * Time (during)	−0.286	0.255	−1.120	0.263
Period (recovery 90) * Time (during)	−0.418	0.299	−1.396	0.163
Period (feeding) * Time (after)	−0.464	0.249	−1.866	0.062
Period (recovery 30) * Time (after)	−0.609	0.276	−2.203	0.028
Period (recovery 60) * Time (after)	−0.750	0.265	−2.827	0.005
Period (recovery 90) * Time (after)	−0.731	0.309	−2.362	0.018
Conditional R^2				0.30
Spatial Attraction				
(Intercept)	−6.789	0.965	−7.037	<0.001
Period (feeding)	5.568	1.113	5.003	<0.001
Period (recovery 30)	7.440	1.103	6.746	<0.001
Period (recovery 60)	8.000	1.090	7.342	<0.001
Period (recovery 90)	3.885	1.117	3.477	<0.001
Time (during)	−4.016	1.134	−3.541	<0.001
Time (after)	−3.305	0.773	−4.277	<0.001
Period (feeding) * Time (during)	5.689	1.160	4.904	<0.001
Period (recovery 30) * Time (during)	−0.522	1.187	−0.439	0.660
Period (recovery 60) * Time (during)	−1.450	1.177	−1.232	0.218
Period (recovery 90) * Time (during)	−0.365	1.242	−0.294	0.769
Period (feeding) * Time (after)	1.140	0.812	1.404	0.160
Period (Recovery 30) * Time (after)	−3.372	0.869	−3.880	<0.001
Period (recovery 60) * Time (after)	−2.398	0.829	−2.892	0.004
Period (recovery 90) * Time (after)	−1.735	0.904	−1.919	0.055
Conditional R^2				0.88

Estimated Period and Time effect coefficients (β) and their standard errors (SE), z values and the individual coefficient type I error estimate (P). Time (during) = 1 h of feeding, Time (after) = 1 h postfeeding, Period (feeding) = feeding month, Period (recovery 30) = first 30 days of recovery, Period (recovery 60) = second 30 days of recovery, Period (recovery 90) = third 30 days of recovery. The baseline level for the factor Period was the baseline month. For the factor Time, the baseline level was the 1 h prefeeding.

the recovery month (Fig. 4, Table 2). Metabolic rates were significantly affected by the interaction between Period and Temperature ($\text{wAIC}_c = 1.00$; Table 2, Appendix Table A4). Across all periods, the metabolic rates increased significantly with temperature. However, they increased at a slower rate during the feeding period than the baseline period. In contrast, they increased significantly faster with temperature during recovery 60 and recovery 90 compared to the baseline period. Despite the significant effect of Period and of the interaction between Period and Temperature, variations were small compared to changes with temperature (Fig. 4).

Changes in Spatial Distribution

The top-ranked model for the comparison of the core area was the Null model ($\text{wAIC}_c = 0.93$; Appendix Table A5). The top-ranked model investigating the extents of the home range included Period as a fixed factor ($\text{wAIC}_c = 0.93$; Appendix Table A5). While there was no significant difference in core areas between periods (Period−RVI = 0.07; Table 3), home range was significantly larger during the first 30 days of recovery compared to the baseline period as well as the last 30 days of recovery (Period−RVI = 0.93; post hoc Tukey: baseline−recovery 30: $\beta = -309718$, $t_{21} = -3.508$, $P = 0.016$; Fig. 5, Table 3).

DISCUSSION

We investigated the impact of daily feeding events on the spatial distribution, activity (as a proxy for energy expenditure) and metabolic rates of juvenile lemon sharks at a site previously unfrequented by humans. Data collection started prior to any feeding events taking place providing the opportunity to collect baseline data, which is often missing in studies assessing the effects of wildlife tourism. Using data collected daily during the 1 h prefeeding, feeding and postfeeding events, we have shown evidence for anticipatory behaviour during prefeeding. Sharks exhibited elevated levels of Burst Activity and spent more time at the feeding site within 27 days of daily feeding events. However, overall daily activity, energy expenditure and broadscale spatial distribution were not affected. Burst Activity returned to baseline levels after the first 30-day recovery period during which feeding events had ceased. In contrast, the spatial association of the feeding site remained for at least 90 days postfeeding. Our findings reveal shark feeding operations may not affect the daily activity and metabolic rates of focal species or their broad distribution but can alter fine-scale spatial distribution patterns. We further found evidence for intraspecific variability with one individual, while being frequently detected on both refuge receivers, never participating in the feeding events. This variability is possibly due to differences in personality (Dhellemmes et al., 2020; Finger, 2019). Similar intraspecific variability with regard to wildlife feeding operations has previously been demonstrated in bull sharks in Fiji (Brunnschweiler & Barnett, 2013).

Anticipatory Behaviour

Anticipation is often used to investigate time−place learning capabilities of organisms by assessing behavioural changes preceding the introduction of a reward or punishment (Gómez-Laplaza

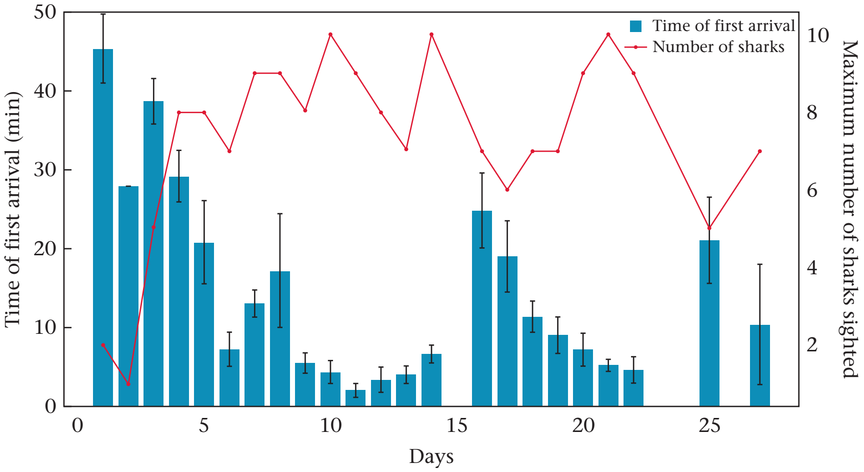

Figure 3. Illustration of the daily mean time of first arrival ± SE (min) following the introduction of the bait box at the feeding site, and the daily maximum number of sharks present during the feeding events.

& Morgan, 2005; Reebs, 1999). While juvenile lemon sharks are known to naturally use the shallow water inlet at Aya's Spot during high tides (Guttridge et al., 2012), we observed a shift in space use inside Aya's Spot as a result of daily feeding events. In the 1 h preceding the feeding event, sharks changed from being predominantly inside Aya's Spot to spending more time at its entrance where feeding events took place. This anticipatory behaviour usually indicates spatial learning linked to a temporal component

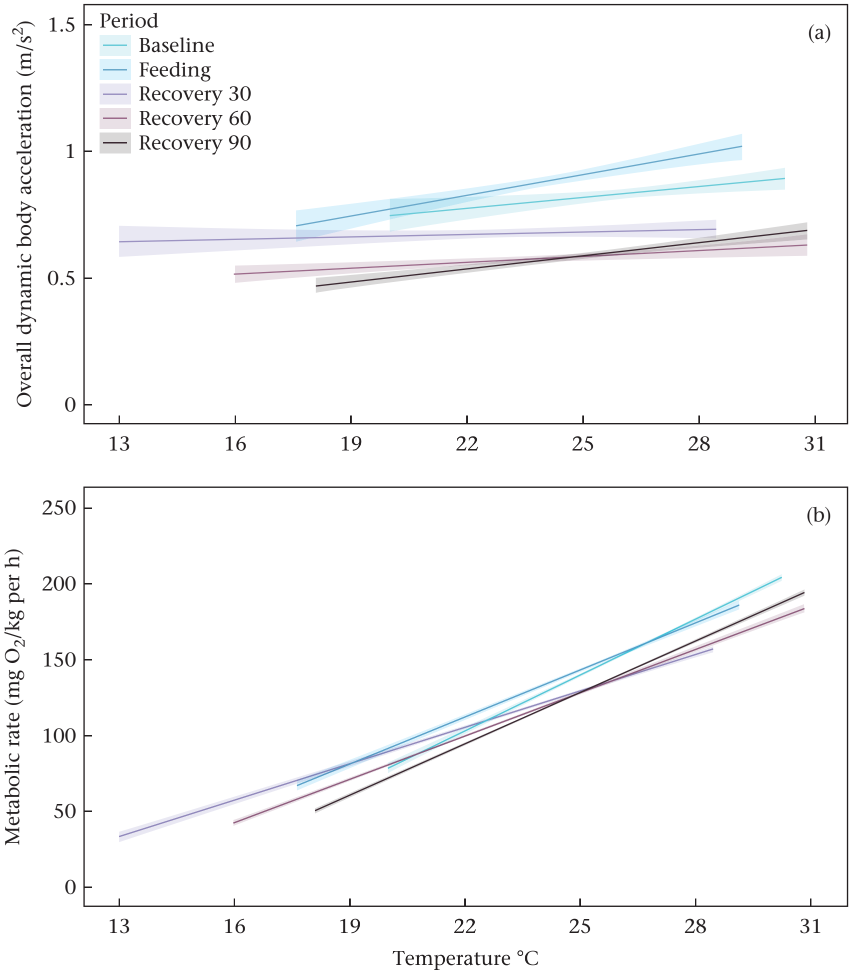

Figure 4. Relationship between (a) the mean daily overall dynamic body acceleration (m/s^2) and (b) the mean daily metabolic rate (mg O$_2$/kg per h) and water temperature. Lines of best fit were applied with 95% confidence intervals for each of the five periods.

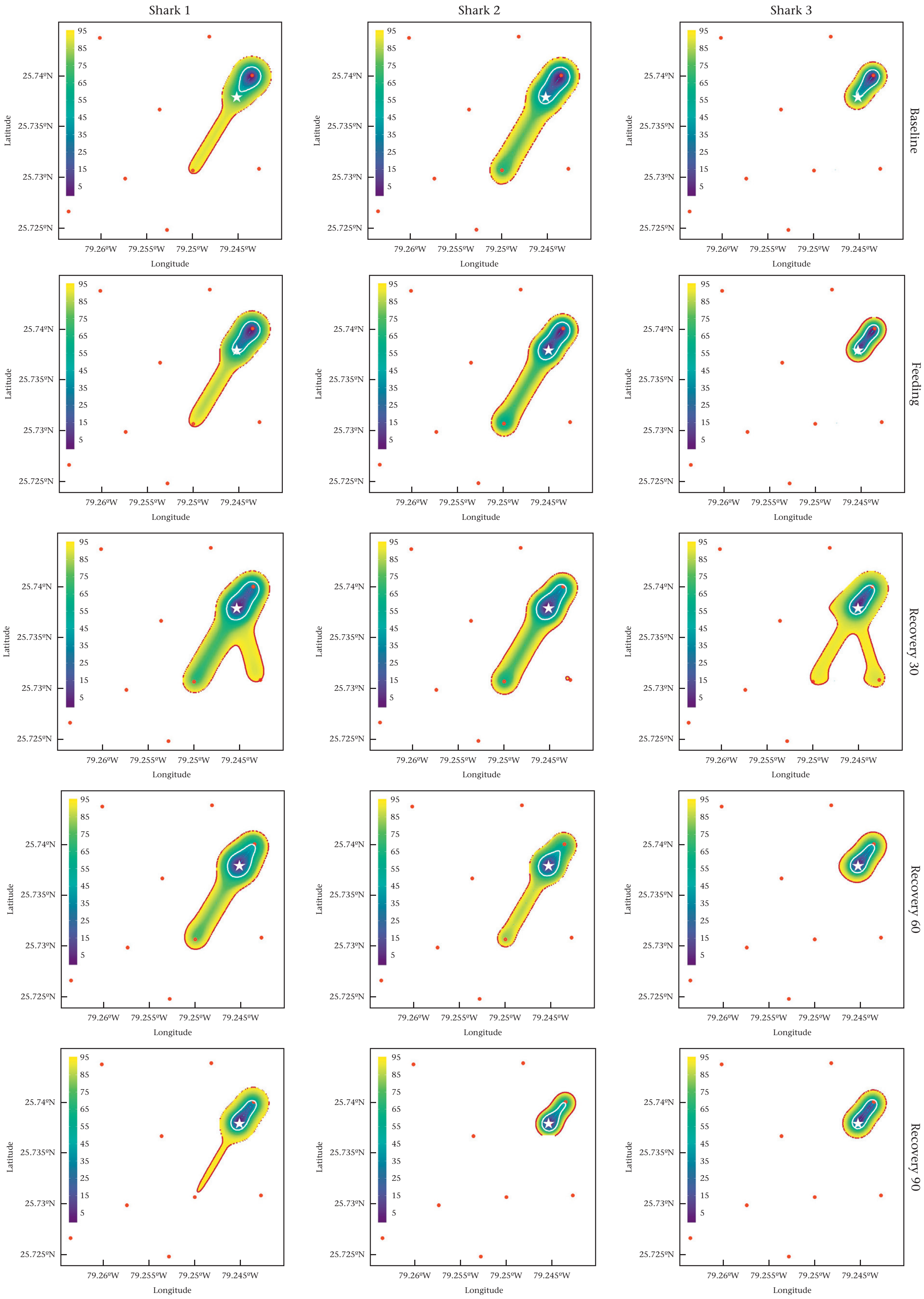

Figure 5. Brownian Bridge kernel utilization density estimates for each individual (sharks 1–6) and each period (baseline, feeding, recovery 30, recovery 60 and recovery 90). The white star marks the receiver located at the feeding site and the red dots mark the positions of the remaining nine receivers. The contours illustrate the core area (white) and the home range (red).

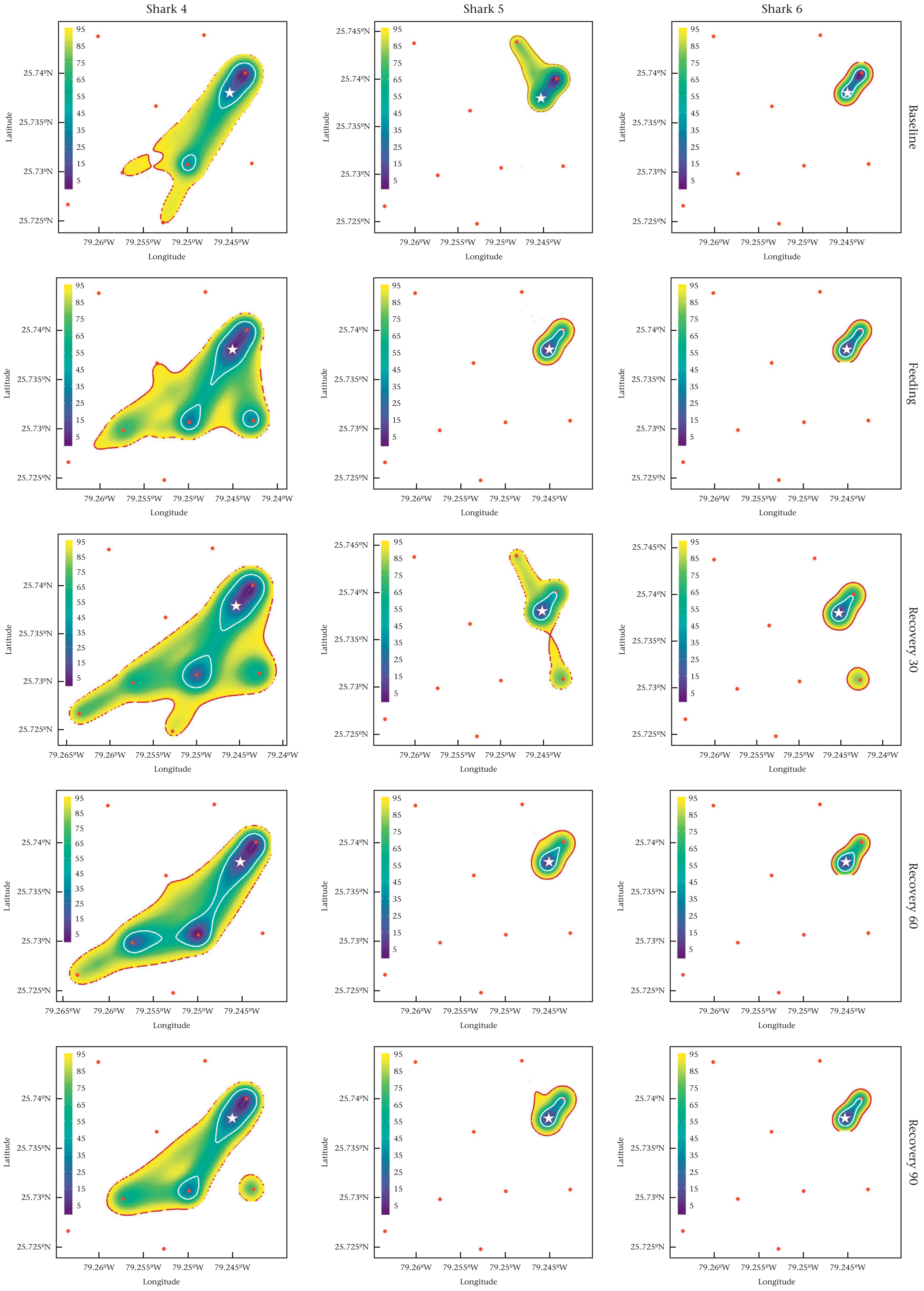

Figure 5. (*continued*).

Table 2
Summary table for the models investigating the Period and Time effects on the mean daily activity and the mean daily metabolic rates

Effect	β	SE	Z	P
Mean daily activity				
(Intercept)	−0.271	0.224	−1.212	0.226
Period (feeding)	0.371	0.282	1.316	0.188
Period (recovery 30)	0.416	0.247	1.690	0.091
Period (recovery 60)	−0.608	0.238	−2.555	0.011
Period (recovery 90)	−0.660	0.239	−2.766	0.006
Temperature	−0.006	0.008	−0.729	0.466
Period (feeding) * Temperature	−0.015	0.011	−1.396	0.162
Period (recovery 30) * Temperature	−0.036	0.009	−3.823	<0.001
Period (recovery 60) * Temperature	0.00002	0.009	0.003	0.998
Period (recovery 90) * Temperature	0.008	0.009	0.883	0.377
Conditional R^2				0.16
Mean daily metabolic rate				
(Intercept)	2.303	0.026	88.79	<0.001
Period (feeding)	0.075	0.033	2.28	0.022
Period (recovery 30)	0.008	0.028	0.28	0.778
Period (recovery 60)	−0.146	0.027	−5.34	<0.001
Period (recovery 90)	−0.132	0.027	−4.83	<0.001
Temperature	0.033	0.001	35.14	<0.001
Period (feeding) * Temperature	−0.003	0.001	−2.20	0.028
Period (recovery 30) * Temperature	−0.002	0.001	−1.45	0.147
Period (recovery 60) * Temperature	0.004	0.001	3.74	<0.001
Period (recovery 90) * Temperature	0.004	0.001	3.45	<0.001
Conditional R^2				0.50

Estimated Period and Temperature effect coefficients (β) and their standard errors (SE), z values of factors included in the model averaging (Appendix Table A4), and the individual coefficient type I error estimate (*P*). Period (feeding) = feeding month, Period (recovery 30) = first 30 days of recovery, Period (recovery 60) = second 30 days of recovery, Period (recovery 90) = third 30 days of recovery. The baseline level for the factor Period was the baseline month.

marked by the rising of the tide. Fish and other organisms are capable of tracking time by reference to an internal clock, which is often set by light cycles (i.e. circadian rhythm) and is maintained even in the absence of external cues (Amaral et al., 2014; Bell-Pedersen et al., 2005; de Almeida Moura, da Silva Lima, Silveira, Miguel, & Luchiari, 2017). Marine organisms, including sharks, are, however, also predisposed to linking behaviour to tidal cycles (Gibson, 2003; Shepard et al., 2006); as a result, associating this natural cycle with feeding for our experiment potentially made it easier for sharks to anticipate the timing of feeding events. Regarding the spatial component of the learning process, juvenile lemon sharks possess an innate homing ability and can successfully return to their home range after being displaced by up to 16 km (Edrén & Gruber, 2005). Many shark species are known to return to a resided-in area after making long-distance movements (e.g. Port Jackson sharks, *Heterodontus portusjacksoni*: Bass et al., 2017), display site fidelity (Bond et al., 2012; Vianna, Meekan, Meeuwig, & Speed, 2013) or return to their exact birth place (i.e. natal philopatry; e.g. lemon sharks: Chapman, Feldheim, Papastamatiou, & Hueter, 2015; Feldheim et al., 2014). Spatial learning has also been demonstrated on a much smaller spatial scale, with grey bamboo sharks, *Chiloscyllium griseum*, being able to locate a goal position inside a maze using a directional strategy or spatial learning based on visual landmarks (Fuss, Bleckmann, & Schluessel, 2014). Given the visual landmarks used in our study, juvenile lemon sharks might have also used a combination of direction strategy and spatial learning to locate the feeding site.

Table 3
Summary table for the models investigating the Period and Time effects on the core areas and home ranges

Effect	β	SE	t	P
Core area				
(Intercept)	88782.69	39492.24	2.248	0.035
Period (feeding)	15955.50	21183.56	0.753	0.460
Period (recovery 30)	32208.30	21183.56	1.520	0.143
Period (recovery 60)	37656.63	20775.68	1.813	0.084
Period (recovery 90)	−1869.02	20775.68	−0.0900	0.929
Conditional R^2				0.15
Home range				
(Intercept)	572388.7	252480.50	2.267	0.034
Period (feeding)	62213.9	88286.02	0.705	0.489
Period (recovery 30)	309717.7	88286.02	3.508	0.002
Period (recovery 60)	81309.6	86651.35	0.938	0.359
Period (recovery 90)	−57849.9	86651.35	−0.668	0.512
Conditional R^2				0.32

Estimated Period effect coefficients (β) and their standard errors (SE), t values of factors and the individual coefficient type I error estimate (P). Period (feeding) = feeding month, Period (recovery 30) = first 30 days of recovery, Period (recovery 60) = second 30 days of recovery, Period (recovery 90) = third 30 days of recovery. The baseline level for the factor Period was the baseline month.

The shift in space use inside Aya's Spot during the 1 h of prefeeding shows that sharks moved close to the feeding site in anticipation of the upcoming feeding event. This is further supported by the simultaneous increase in Burst Activity. Based on time at first arrival and number of sharks sighted, juvenile lemon sharks required 5–10 days to start anticipating feeding events and ca. 11 days to reach the learning criterion. This learning period is similar to that of bamboo sharks trained to locate a goal inside a maze (ca. 8 days; Fuss et al., 2014) and Port Jackson sharks trained in a spatial task (ca. 15 days; Heinrich, Vila Pouca, Brown, & Huveneers, 2020). Anticipation of a feeding event and subsequent spatial learning have also been demonstrated in bull sharks (Brunnschweiler & Barnett, 2013) and short-tail stingrays, *Bathytoshia brevicaudata* (Pini-Fitzsimmons, Knott, & Brown, 2018). Following ca. 30 years of fish frames being frequently discarded at a boat ramp cleaning station, short-tail stingrays consistently visited the boat ramp in late afternoon when fish cleaning typically occurred, regardless of whether fish cleaning was taking place. This suggests that these rays anticipate afternoon feeds as a result of a learnt time–place association (Pini-Fitzsimmons et al., 2018).

Despite small declines in anticipation following periods of inclement weather when we were unable to feed sharks, some anticipation was still observed well after the feeding events had fully ceased. For instance, Burst Activity was still significantly higher than baseline levels during the first 30 days of recovery. Spatial anticipation lasted even longer, with sharks still spending more time at the feeding site during the 1 h feeding event after 60–90 days of recovery compared to the baseline period. Our results suggest that a learnt spatial association can be retained for extended periods in wild populations of elasmobranchs. Indeed, laboratory studies on memory retention capacities demonstrated that sharks can memorize learnt behaviours for long periods of time. Juvenile grey bamboo sharks remembered a learnt visual discrimination task for up to 50 weeks in the absence of reinforcement (Fuss & Schluessel, 2015). Similarly, Port Jackson sharks retained a learnt association with air bubbles for up to 40 days (Guttridge & Brown, 2013). However, the extent of memory retention and extinction rates in elasmobranchs requires further studies in more controlled environments.

Daily Activity and Metabolic Rates

The increased activity prior to and during the feeding period was not sufficient to affect sharks' daily overall dynamic body acceleration and metabolic rate. These results contrast with a previous study showing that wildlife tourism targeting reef sharks increased the amount of time whitetip reef sharks spent swimming and subsequently their daily overall dynamic body acceleration (Barnett et al., 2016). The discrepancy between Barnett et al.'s

(2016) study and ours is probably because whitetip reef sharks typically spend most of the day resting on the sea floor (Barnett et al., 2016; Fitzpatrick et al., 2011), similar to other benthic sharks like the Port Jackson shark (Kadar, Ladds, Mourier, Day, & Brown, 2019). The increased activity of whitetip reef sharks due to tourism occurs during the day when these sharks would normally be resting. If they had been fed in the evening when they are naturally active, feeding events would probably have had little perceivable impact on their activity levels and hence energy budget. Although lemon sharks are able to rest on the benthos, they spend most of their time swimming (Bouyoucos, Suski, Mandelman, & Brooks, 2018), and the slight increase in activity during periods when sharks are normally active and swimming was not sufficient to substantially affect routine metabolic rates. This suggests that species that are naturally more active, such as pelagic species, are less likely to be affected by wildlife tourism events at the level of their metabolic rates than benthic species that would naturally rest during the day.

In the absence of a significant effect on shark activity, the observed differences in metabolic rates were driven primarily by changes in ambient water temperatures. This was expected, as temperature is the most important external factor determining energy expenditure in ectotherms like sharks, with basal or standard metabolic rates of ectotherms doubling to tripling with every 10 °C increase in temperature (Clarke & Johnston, 1999; Gillooly, Brown, West, Savage, & Charnov, 2001). While the interaction between temperature and period seemed important in the model, the effect size was relatively small and did not exceed the variation in metabolic rate that occurs throughout the day in lemon sharks (Bouyoucos et al., 2018). Given the extent of the temperature effect on the metabolic rates of sharks, it appears unlikely that short, daily feeding events (ca. 1 h) is substantial relative to the temperature effect. This line of reasoning leads us to conclude that the effect of feeding events will be most apparent at times of stable ambient temperatures.

Spatial Distribution and Fine-Scale Movement Patterns

The broad space use (core area and home range) of juvenile lemon sharks was not influenced by 1 h daily feeding events. Within Aya's Spot, however, there was a clear shift in space use towards the feeding site. The shift lasted for at least 90 days after feeding cessation, further illustrating an extended learning extinction period in these sharks. It also demonstrates that a feeding period as short as 27 days can have significant, long-lasting effects on the fine-scale space use of juvenile sharks. Previous studies support our results, even though most were carried out at well-established feeding sites (Brunnschweiler & Baensch, 2011; Clua, Buray, Legendre, Mourier, & Planes, 2010; Corcoran et al., 2013). For instance, Brunnschweiler and Barnett (2013) demonstrated a change in the fine-scale movements of bull sharks at a feeding site in Fiji with sharks visiting the feeding site for more extended periods on feeding days than on nonfeeding days (Brunnschweiler & Barnett, 2013). The extended home range during the first 30 days of recovery could indicate that sharks were searching for the former feeding site landmarks in the area surrounding Aya's Spot in case the feeding site had moved. Once they were satisfied that the feeding location was nowhere to be found their home ranges returned to baseline levels.

The number of sharks present at the feeding site increased from only three at the start of the daily feeding events (two tagged, one untagged) to ca. 10 within 10 days of feeding. Of the maximum number of 10 sharks we observed during feeding, six were tagged and four were untagged. The recruitment we observed at Aya's Spot during the feeding events might be linked to social learning, which has previously been demonstrated in elasmobranchs (Pouca, Heinrich, Huveneers, & Brown, 2020; Thonhauser et al., 2013), including juvenile lemon sharks (Guttridge et al., 2013). Increases in shark abundance are commonly reported at feeding sites, such as with bull sharks in Fiji (Brunnschweiler, Abrantes, & Barnett, 2014) and southern stingrays, *Dasyatis americana*, in the Grand Cayman Islands (Corcoran et al., 2013; Semeniuk & Rothley, 2008). These changes in abundance can have severe, detrimental effects on the health of the animals, including increased parasite loads, increased conspecific bites and a reduced overall condition (Corcoran et al., 2013; Semeniuk & Rothley, 2008). However, the southern stingray is the only species of elasmobranchs that has so far been reported to suffer such severe detrimental effects from wildlife tourism operations (Trave, Brunnschweiler, Sheaves, Diedrich, & Barnett, 2017). Furthermore, given the natural group-living conditions that juvenile lemon sharks are exposed to daily inside Aya's Spot, it is unlikely they would suffer from the same effects, at least not to the extent witnessed in southern stingrays.

Conclusion

The short feeding period of only 27 days had a significant impact on the fine-scale movement pattern and the Burst Activity of juvenile lemon sharks, indicating that sharks are able to learn associations at a similar rate in natural and laboratory conditions (Fuss & Schluessel, 2015; e.g. ; Guttridge & Brown, 2013). Daily feeding events may result in quick behavioural changes via conditioning, which may be retained for at least 90 days in the absence of any further reinforcement. These responses, in particular the changes in fine-scale spatial distribution, appear to be similar across different species (Barnett et al., 2016; Brunnschweiler & Barnett, 2013; Corcoran et al., 2013). In contrast, the physiological response, metabolic rate, was not substantially affected, and this was probably due to feeding events occurring at times when lemon sharks are naturally active. The ability to collect baseline data prior to the initiation of daily feeding events replicating standard tourism operations provided a unique opportunity to assess how wildlife tourism affects shark behaviour. Our study shows that, while changes in shark behaviour were observed, these changes were spatially restricted and only occurred close to the feeding event. Some of the observed local effects were, however, long lasting. In conclusion, our experiment had minimal effects on the metabolic rate of juvenile lemon sharks, but managers of wildlife tourism industries should consider the potential impacts of long-lasting changes in shark behaviour, even if they are likely to be localized to the feeding site and time. However, the small sample size of our study needs to be taken into consideration. While our results indicate possible effects of feeding activities on the behavioural ecology and spatial distribution of sharks they do not necesseraily apply to all species and indiviuals equally. This is shown by the individual we tagged that, despite being present inside Aya's Spot on feeding days, never participated in any of the feeding events. We therefore recommend to run small-scale pilot studies on target species/populations before establishing new feeding operations to ensure the most sustainable strategies are applied and the negative impacts are minimized.

Author Contributions

All authors contributed to the study design. D.H., F.D., M.S. and T.G. set up the experiments. D.H. collected the data with the help of the station's volunteers, ran the statistical analysis and drafted the manuscript. All authors revised the manuscript, gave final approval and are accountable for accuracy.

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Appendix

Table A1

Ranking of all models assessing the Burst Activity and Spatial Attraction

Model	*df*	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	$\mathrm{wAIC_c}$
Burst Activity				
Period * Time	17	6784.22	0.00	1.00
Period + Time	9	6837.05	52.83	0.00
Period	7	6901.02	116.79	0.00
Time	5	6973.35	189.13	0.00
(Null)	3	7040.76	256.53	0.00
Spatial Attraction				
Period * Time	17	3201.46	0.00	1.00
Period + Time	9	3734.01	532.54	0.00
Time	5	3803.25	601.79	0.00
Period	7	5236.55	2035.09	0.00
(Null)	3	5298.49	2097.03	0.00

$\mathrm{AIC_c}$ = Akaike's information criterion corrected for small sample size, $\Delta\mathrm{AIC_c}$ = the difference in $\mathrm{AIC_c}$ between the current and the top-ranked model, $\mathrm{wAIC_c}$ = model probability. Shark ID and Day were included as random factors in all models. For models that contained an interaction, single factors were also included, but not listed in the table.

Table A2

Ranking of all possible models assessing the Burst Activity and Spatial Attraction around the night-time high tides

Model	*df*	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	$\mathrm{wAIC_c}$
Burst Activity				
Period + Time	9	6737.80	0.00	0.9
Period * Time	17	6742.23	4.43	0.1
Period	7	6753.85	16.05	0.0
Time	5	6833.71	95.91	0.0
(Null)	3	6849.95	112.15	0.0
Spatial Attraction				
Period * Time	17	3292.33	0.00	1.0
Period + Time	9	3335.21	42.88	0.0
Time	5	3374.58	82.25	0.0
Period	7	4525.02	1232.69	0.0
(Null)	3	4561.03	1268.70	0.0

$\mathrm{AIC_c}$ = Akaike's information criterion corrected for small sample size, $\Delta\mathrm{AIC_c}$ = the difference in $\mathrm{AIC_c}$ between the current and the top-ranked model, $\mathrm{wAIC_c}$ = model probability. Shark ID and Day were included as random factors in all models. For models that contained an interaction, single factors were also included, but not listed separately in the table.

Table A3

Summary table for the models investigating the Period and Time effects on the Burst Activity and Spatial Attraction around night-time high tides

Effect	β	SE	*Z*	*P*
Burst Activity				
(Intercept)	−0.923	0.227	−4.072	<0.001
Period (feeding)	0.130	0.243	0.534	0.593
Period (recovery 30)	−0.765	0.227	−3.368	<0.001
Period (recovery 60)	−1.006	0.226	−4.449	<0.001
Period (recovery 90)	−1.401	0.253	−5.542	<0.001
Time (during)	−0.165	0.176	−0.942	0.346
Time (after)	−0.232	0.180	−1.288	0.198
Period (feeding) * Time (during)	0.0549	0.263	0.209	0.834
Period (recovery 30) * Time (during)	0.0423	0.268	0.158	0.875
Period (Recovery 60) * Time (during)	−0.174	0.272	−0.640	0.522
Period (recovery 90) * Time (during)	−0.00973	0.285	−0.034	0.973
Period (feeding) * Time (after)	−0.499	0.270	−1.850	0.064
Period (recovery 30) * Time (after)	0.0127	0.256	0.050	0.960
Period (recovery 60) * Time (after)	−0.176	0.261	−0.676	0.499
Period (recovery 90) * Time (after)	−0.0272	0.284	−0.096	0.924
Conditional R^2				0.16
Spatial Attraction				
(Intercept)	−2.437	0.854	−2.853	0.004
Period (feeding)	0.768	1.012	0.759	0.448
Period (recovery 30)	4.044	0.953	4.243	<0.001
Period (recovery 60)	3.781	0.940	4.023	<0.001
Period (recovery 90)	−0.531	0.982	−0.541	0.589
Time (during)	−4.101	0.546	−7.516	<0.001
Time (after)	−5.029	0.572	−8.798	<0.001
Period (feeding) * Time (during)	0.137	0.713	0.193	0.847
Period (recovery 30) * Time (during)	−0.637	0.675	−0.943	0.345
Period (recovery 60) * Time (during)	1.348	0.590	2.284	0.022
Period (recovery 90) * Time (during)	0.502	0.672	0.746	0.456
Period (feeding) * Time (after)	−0.858	0.871	−0.984	0.325
Period (recovery 30) * Time (after)	−0.644	0.694	−0.927	0.354
Period (recovery 60) * Time (after)	1.977	0.603	3.280	0.001
Period (recovery 90) * Time (after)	0.924	0.656	1.408	0.159
Conditional R^2				0.86

Estimated effect coefficients (β) and their standard errors (SE), *z* values and the individual coefficient type I error estimate (*P*). Time (during) = 1 h of feeding, Time (after) = 1 h postfeeding, Period (feeding) = feeding month, Period (recovery 30) = first 30 days of recovery, Period (recovery 60) = second 30 days of recovery, Period (recovery 90) = third 30 days of recovery. The baseline level for the factor Period was the baseline month. For the factor Time, the baseline level was the 1 h prefeeding before the feeding event.

Table A4

Ranking of all possible models assessing the mean daily activity and mean daily metabolic rates

Model	*df*	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	$\mathrm{wAIC_c}$
Mean daily activity				
Period * Temperature	27	111285.3	0.00	1.00
Period + Temperature	23	111326.4	41.19	0.00
Temperature	19	111342.5	57.22	0.00
Period	22	111350.9	65.65	0.00
(Null)	18	111366.9	81.67	0.00
Mean daily metabolic rates				
Period * Temperature	13	−80668.84	0.00	1.00
Period + Temperature	9	−80584.77	84.07	0.00
Temperature	5	−80473.31	195.53	0.00
Period	8	−68614.08	12054.76	0.00
(Null)	4	−68534.66	12134.18	0.00

$\mathrm{AIC_c}$ = Akaike's information criterion corrected for small sample size, $\Delta\mathrm{AIC_c}$ = the difference in $\mathrm{AIC_c}$ between the current and the top-ranked model, $\mathrm{wAIC_c}$ = model probability. Shark ID was included as a random factor in all models. For models that contained an interaction, single factors were also included, but not listed separately in the table.

Table A5
Ranking of all possible models assessing the core areas and home ranges

Model	*df*	AIC_c	ΔAIC_c	$wAIC_c$
Core area				
Null	3	795.68	0.00	0.93
Period	7	800.78	5.1	0.07
Home range				
Period	7	898.66	0.00	0.93
Null	3	903.77	5.1	0.07

AIC_c = Akaike's information criterion corrected for small sample size, ΔAIC_c = the difference in AIC_c between the current and the top-ranked model, $wAIC_c$ = model probability. Shark ID was included as a random factor in all models.

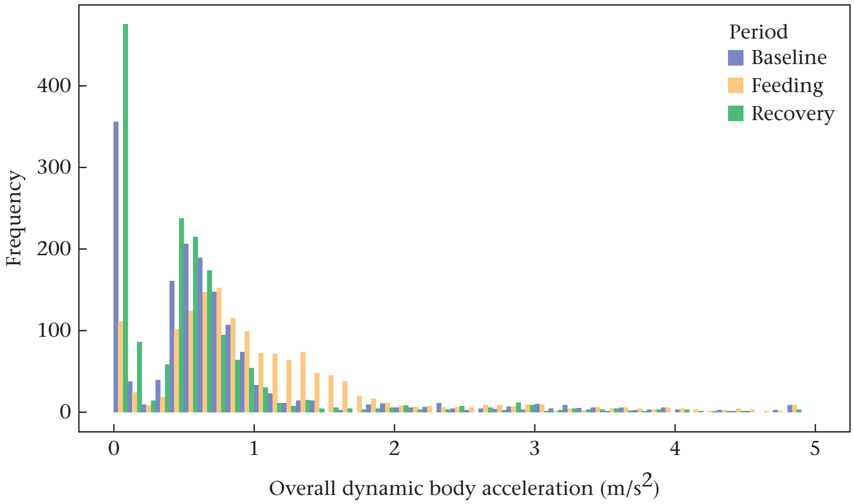

Figure A1.Frequency distribution of shark overall dynamic body acceleration across the baseline, feeding and combined recovery periods. The data used only included the three 1 h windows of the daytime high tides we focused on during our investigation of the anticipatory behaviour of the sharks.

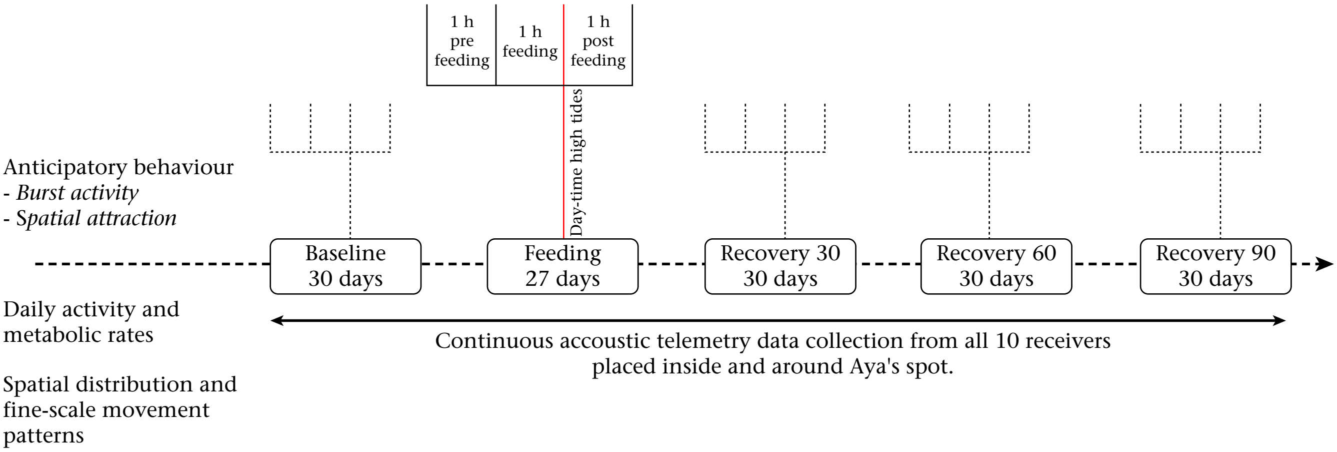

Figure A2. Experimental timeline, showing the length of each of the five periods and illustrating the 3 h window around the high tides.

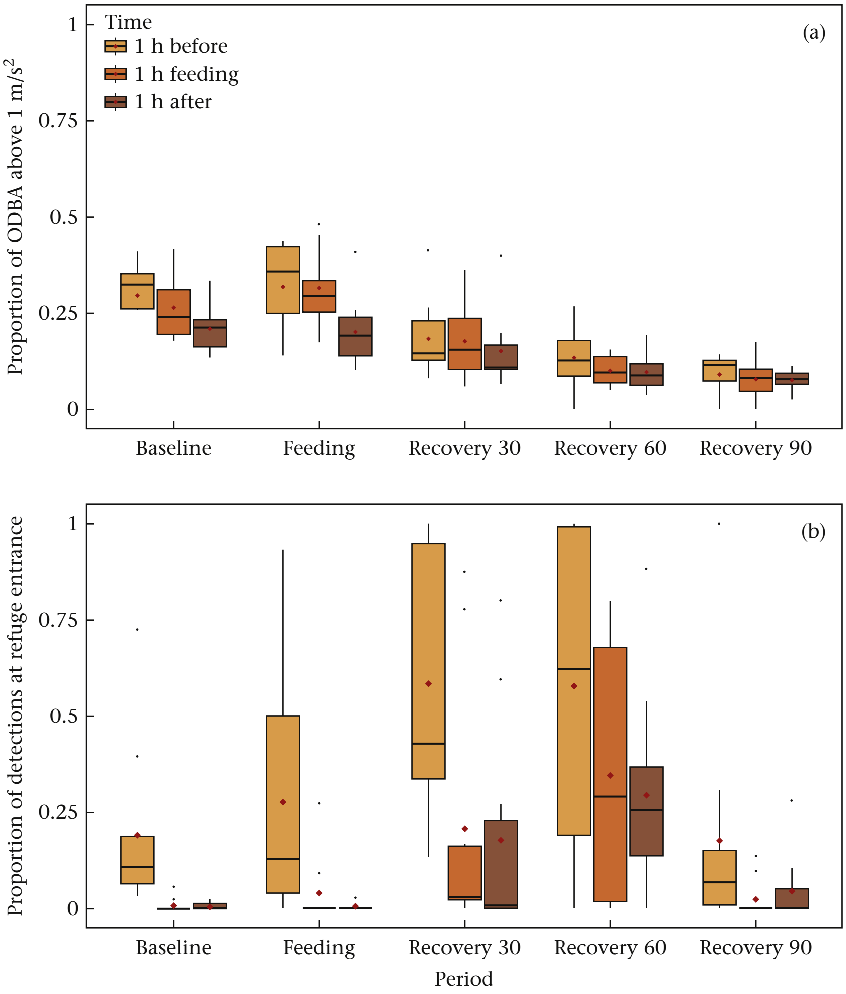

Figure A3. Box plot illustrating (a) the proportion of overall dynamic body acceleration (ODBA, m/s^2) above 1 m/s^2, and (b) the proportion of detections made at the refuge entrance during prefeeding, feeding and postfeeding around the night-time high tides plotted against the Period. The horizontal lines inside the boxes mark the median and the red diamonds the mean for 1 h before, during and after feeding events. The upper and lower boundaries of the box represent the third and first quartiles. The whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.