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## Home Range of Juvenile Lemon Sharks, *Negaprion brevirostris*

JOHN F. MORRISSEY AND SAMUEL H. GRUBER

**Manual acoustic telemetry techniques were used to study spatial and temporal patterns of movement of juvenile lemon sharks. Ultrasonic transmitters were implanted into the coelom of 38 sharks, yielding trackings totaling 2281 telemetry fixes. Activity space varied from 0.23 km<sup>2</sup> to 1.26 km<sup>2</sup> and was positively correlated with shark size. Three indices of site attachment demonstrated that juvenile lemon sharks establish a home range. An index of site defense and field observations indicated that no territoriality was observed against conspecifics.**

**R**EQUISITE to understanding a species is an understanding of patterns of activity and use of space (Tester and Siniff, 1965; Weatherhead and Hoysak, 1989). Spatial and temporal patterns have implications for energetics, social behavior, and reproduction within a population (Gregory et al., 1987). An inherent property of most vertebrate activity spaces is that they are spatially and temporally stable (for various durations) and are repeatedly traversed (Calhoun and Casby, 1958; Winter, 1977). We consider "home range" to be "the spatially and temporally defined area (Odum and Kuenzler, 1955) over which an animal travels while engaged in its normal activities" (McNab, 1963; Jewell, 1966).

Estimation of the area of a home range has been recommended for life-history studies (Schoener, 1981; Bowen, 1982; Braun, 1985) because properties of the activity space (e.g., size and shape) should have adaptive significance. When coupled with ecological and behavioral information, the size and shape of an activity space become meaningful (Bowen, 1982) because factors that influence home range (such as distribution of food or cover) become apparent (Waldschmidt, 1979).

Bioenergetic considerations are considered of primary importance in determining the size of an activity space (Gaines and Johnson, 1982; Shank, 1986). The optimization of reproductive success involves maximizing the ratio of benefits and costs associated with selecting an

optimally sized activity space (Maynard-Smith, 1974). Therefore, it has been suggested that an animal shall occupy the smallest area that satisfies all of its energetic needs (Maza et al., 1973; Abramsky and Tracy, 1980).

In 1963, McNab developed his classic model relating size of activity space to body size. Due to the breadth of McNab's (1963) model, it is one of the most studied relationships in ecology (Cameron and Spencer, 1985). In his review, Shank (1986) cited the following evidence supporting McNab's (1963) model: (1) animals utilizing sparse resources (i.e., carnivores) have large home ranges (Harestad and Bunnell, 1979; Harvey and Clutton-Brock, 1981; Gittleman and Harvey, 1982); (2) certain intertaxa differences in size of activity space can be explained by differences in metabolic rates (Mace and Harvey, 1983); (3) individuals in groups have larger activity spaces than solitary animals because resources must be shared more directly (Milton and May, 1976; Damuth, 1981a, 1981b); and (4) more productive habitats allow for smaller activity spaces (Harestad and Bunnell, 1979).

Not all workers agree with McNab's (1963) simple model. Several showed size of home range not correlated with body size (e.g., Maza et al., 1973) or negatively correlated with body size (e.g., Schoener and Schoener, 1982; Fish and Savitz, 1983). Reiss (1988) concluded that "we are still a considerable way from understanding why animals have the home range that they do."

To our knowledge, only five studies have ex-

amined the relationship between home range and body size in fishes, with highly variable results (Fish and Savitz, 1983; Miller and Menzel, 1986; Strong, 1989; Todd and Rabeni, 1989; Grant and Kramer, 1990). Moreover, although several species of elasmobranchs have been tracked (see review by Nelson, 1990), few workers estimated area of home range.

Therefore, we examined the spatial and temporal patterns of activity of juvenile lemon sharks, *Negaprion brevirostris* (Poey), via acoustic telemetry. This study provides the first statistically valid estimate of size of the home range of any elasmobranch species. In all previous studies, logistics (e.g., life of transmitters, weather), and not statistical considerations, determined sample size. The present study is the first to utilize nonarbitrary sampling in examining patterns of movement, degree of site fixity and defense, and the correlation between size of home range and body size in any elasmobranch.

#### MATERIALS AND METHODS

*Study site.*—This study was conducted at Bimini, Bahamas, a subtropical island cluster on the western edge of the Great Bahamas Bank approximately 86 km due east of Miami, Florida (Newell and Imbrie, 1955). Tracking operations were performed in Bimini Lagoon and the North Sound. Bimini Lagoon occupies approximately 21 km<sup>2</sup> and is bordered on the west and north by the V-shaped island of North Bimini, and to the south by South Bimini. The North Sound occupies approximately 3 km<sup>2</sup> and is located within the apex of North Bimini. Additional detailed descriptions of the hydrological, geological, and ecological characteristics of Bimini Lagoon and the North Sound are given by Newell and Imbrie (1955) and Jacobsen (1987).

*Telemetry equipment.*—Crystal-controlled, high-power, ultrasonic (68.1–78.1 kHz) transmitters (XTAL-87; Sonotronics, Inc., Tucson, Arizona) were surgically implanted in all sharks. The cylindrical transmitters were 16 mm × 66 mm, weighing 21 g (i.e., about 1.8% of the smallest shark telemetered), and had a volume of 13.3 cc. Transmitters were activated by a magnetic reed switch.

Transmitter output was monitored with two types of manual receivers (USR-4D and USR-5; Sonotronics, Inc., Tucson, Arizona). Both units were direct conversion types equipped with DH-2 directional hydrophones with a sensitivity

of -84 dBV (re 1 microbar at one meter) and a beam width of ±6 degrees at half power points.

*Capture of sharks.*—Juvenile lemon sharks were either (1) entangled in a monofilament gill net deployed perpendicular to the shoreline at the water's edge; (2) chased down by a power boat and dip-netted out of the water; or (3) hooked on a 200-pound test monofilament longline. All captive sharks were maintained until needed in the North Sound in pens constructed of galvanized chain-link or flexible polyvinylchloride fencing.

*Surgical procedure.*—All transmitters and surgical tools were held in 75 percent isopropanol for approximately 20 min prior to surgery (Harvey et al., 1984). Each shark was removed from the pen and placed in a 1:20,000 bath of tricaine methane sulfonate (MS-222) anesthetic until no response could be elicited from the shark (Ziebell, 1973; Chisholm and Hubert, 1985). A 3–4 cm incision was made through the abdominal wall anterior to the origin of one pelvic fin. Transmitters then were inserted into this incision and pushed cranial until they were completely within and against the dorsal wall of the peritoneal cavity. The incision was closed with 3-0 Coated Vicryl (Ethicon, Inc.) absorbable suture material. Finally, the shark was returned to the pen, and "walked" until it swam on its own (approximately 2–5 min). The shark was released after 24 h.

*Tracking procedure.*—Manual tracking followed standard procedures as detailed by Ireland and Kanwisher (1978). The tracking craft was towed by the wading tracker to preclude the possibility of engine noise altering the behavior of the telemetered shark (Stasko and Buerkle, 1975).

Twenty-four landmark flags, placed around the study site on permanent moorings, were used with standard triangulation procedures (Mech, 1983) during tracking sessions to estimate the location of the tracking craft. Areal error of the triangulation-derived polygon was calculated as the mean area of all polygons (Saltz and White, 1990). We then estimated shark-to-boat distance and direction by listening to signal bearing and strength.

Each tracking session consisted of following one telemetered shark continuously for 6 h. We obtained fixes of location at 15-min intervals during each 6-h session. This interval was selected (1) because of its common usage (e.g., McCleave et al., 1977; Dombeck, 1979; Gruber et al., 1988) making these data directly comparable to the results of many other studies

(Rose, 1982), and (2) to facilitate calculation of activity space parameters other than area (e.g., time budget analysis, rate of movement, and temporal space use). Following the observation-area procedure of Odum and Kuenzler (1955), we terminated data collection for an individual shark when an additional 6-h tracking session (i.e., 24 fixes) produced a <10% increase in estimated area [see also Bowen (1982) and Mesnier and Barrette (1982)]. Five or six tracking sessions, which included data from all times of day and night, typically comprised a complete experiment for one shark.

*Calculation of parameters of home range.*—Geometric centers of activity (COA) were calculated for each activity space by using the following formula:

$$\text{COA} = X/Y$$

where X = the mean of all X-coordinates and Y = the mean of all Y-coordinates for all locations of a particular shark (Hayne, 1949). As a mean of X/Y coordinates, the COA does not represent a site of biological significance and even may be found outside of the known activity space (Hayne, 1949; Tester and Siniff, 1965). However, it is useful when calculating other parameters of activity space, such as Activity Radii (see below).

We estimated the area of each individual's home range by using a modification of the minimum convex polygon (MCP) method (Dalke, 1942; Mohr, 1943; Winter, 1977). Without modification, the MCP method may result in an overestimation of the true size of an activity space because the resulting polygons may contain unutilized areas (Anderson, 1982; Braun, 1985) or may include unusual jaunts made by the subject (Brown and Orians, 1970; Maza et al., 1973). We modified the MCPs in two ways to reduce the possibility of areal overestimation. First, we did not include uninhabitable areas (i.e., land) in the MCPs that we drew. This first modification typically resulted in the shoreline being one boundary for the polygon and/or the construction of a polygon which was not convex (Winter and Ross, 1981; Mesing and Wicker, 1986). Second, we excluded objectively all unusual excursions by deleting 5% of the observations which were furthest from the COA, thus creating a 95% MCP (Stickel, 1954; Jorgensen, 1968).

We calculated an Index of Eccentricity (ECC) as a representation of the shape of a home range:

$$\text{ECC} = l/w$$

wherein  $l$  = maximum length of the activity

space and  $w$  = maximum width of the activity space (Ables, 1969). An ECC = 1 indicates a symmetrical (e.g., circular) activity space and values of ECC > 1 characterize an increasingly asymmetrical activity space (Spencer et al., 1990).

We calculated the following three indices of site attachment: (1) A Linearity Index (LI; Bell and Kramer, 1979):

$$\text{LI} = (F_n - F_1)/D$$

where  $F_n$  is the location of the last fix taken for an animal,  $F_1$  is the location of the first fix recorded for an animal and  $D$  is the total distance traveled by the animal. This index indicates linear paths without revisitation of a region (LI = 1) or meandering reuse of a home range (LI < 1).

(2) Index of Reuse [IOR; modified from Cooper (1978) and McKibben and Nelson (1986)]:

$$\text{IOR} = [\text{OV}(A1 + A2)]/(A1 + A2)$$

where  $[\text{OV}(A1 + A2)]$  is the area of overlap between two daily (i.e., 6-h) home ranges and  $(A1 + A2)$  is the total area of both home ranges. This index ranges from zero (i.e., no overlap, nomadic behavior) to one (i.e., complete overlap, extreme site attachment).

(3) Activity Radii (AR) from the COA, similar to  $r^2$  of Schoener (1981) and Mean Squared Distance of Spencer et al. (1990):

$$\text{AR} = [(x_i - x)^2 + (y_i - y)^2]^{1/2}$$

where  $x$  and  $y$  are the coordinates of the geometric center of activity. This index measures the distribution of activity throughout a home range (Calhoun and Casby, 1958). AR values less than the length of the home range suggest intensive use of core areas or site fidelity.

We also used the IOR as an index of overlap between the home ranges of neighboring conspecifics (Hawkins et al., 1974) to estimate the degree of sociability between two individuals. An IOR value of zero reflects complete exclusion of conspecifics over a given time frame and a value of one reflects complete overlap between neighboring sharks.

## RESULTS

Ultrasonic transmitters were implanted into 22 male and 16 female juvenile lemon sharks ranging in precaudal length (PCL) from 46.8–100.6 cm. Tracking operations occurred from Feb. 1987 to Dec. 1989. The interval between the first and the last 6-h session for one individual ranged from 1–153 days. From 5–162

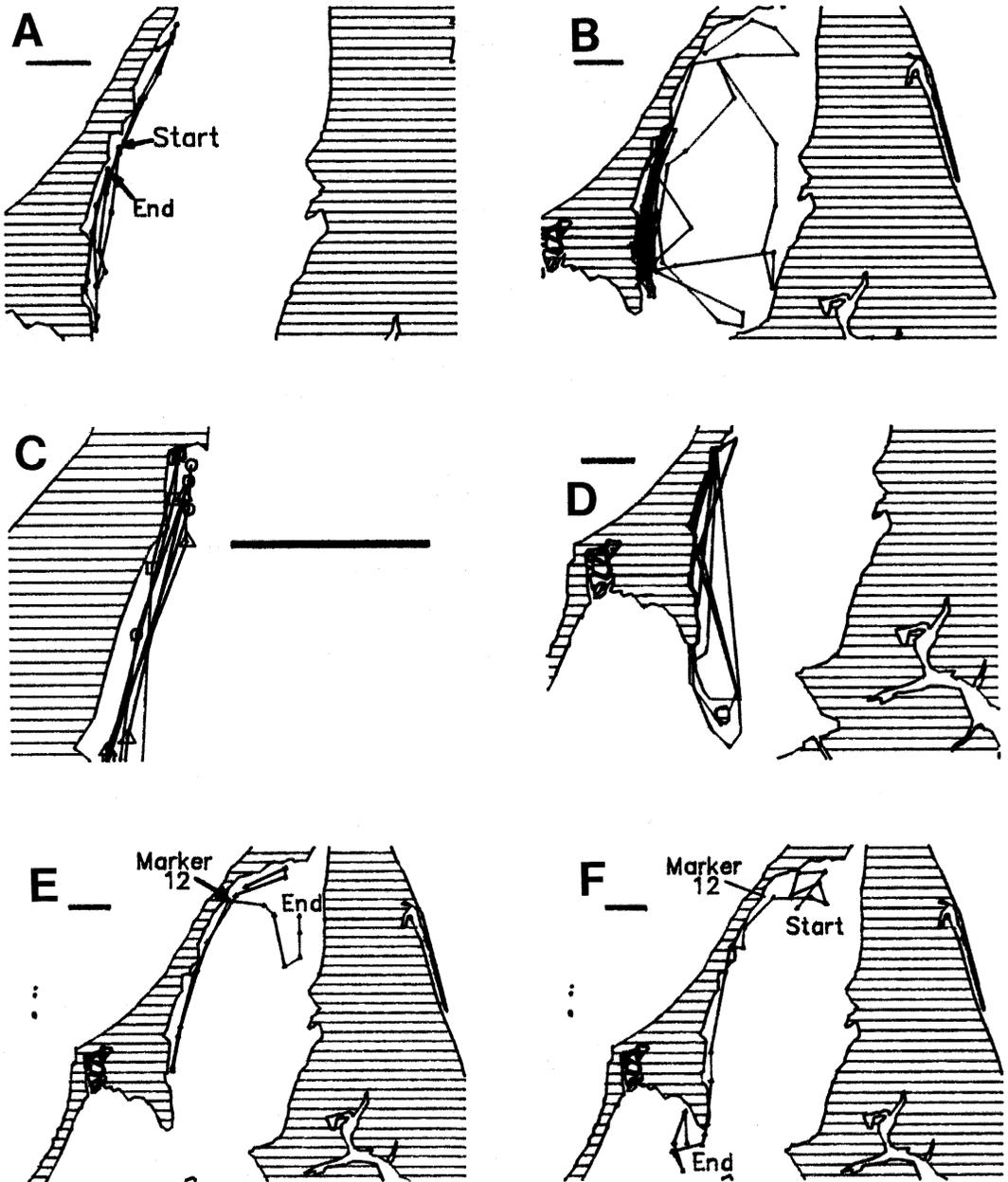


Fig. 1. Exemplary patterns of movement of juvenile lemon sharks at Bimini, Bahamas. All scale bars are 350 m and all fixes represent 15-min intervals. (A) Movements during a six-hour tracking session of Shark #17 on 19 Dec. 1989; (B) All recorded locations (151) for Shark #35 during June–July 1988; (C) Magnification of Figure 1B (circles are daytime telemetry fixes, squares are nighttime points, and triangles are twilight locations); (D) MCPs for all tracking sessions of Shark #23; (E) Track of Shark #31 on 13 Aug. 1988; (F) Track of Shark #31 on 22 Aug. 1988.

positional fixes were collected per shark. A total of 2281 fixes were obtained: 1545 in daylight and 736 at night.

Seventeen telemetered sharks were recaptured after 8–1055 days, growing from  $-0.3$ – $28.2$  cm PCL ( $-6.4$ – $9.9$  cm/yr). Seven were at liberty more than 75 days and grew an average

of  $6.7$  cm/yr (range =  $3.3$ – $9.9$  cm/yr). All sharks had normal color and muscle tone and appeared healthy when recaptured. Implantation wounds healed quickly. After about 20 days, only a thin black line was present at the site of the incision. After five months, the incision was nearly indistinguishable. None of the implanted trans-

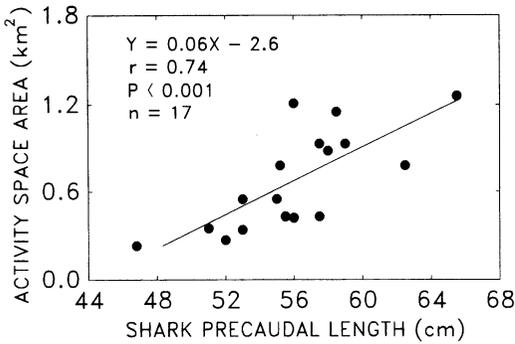


Fig. 2. Relationship between area of activity space of 17 juvenile lemon sharks (as estimated via the 95% MCP technique) and their precaudal length.

mitters were encapsulated by peritoneal membranes.

Figure 1A–D illustrates typical movement patterns of tagged juvenile lemon sharks. Most sharks tracked usually swam within 50 m of the shoreline, executing repeated, greatly attenuated, horizontal loops in a consistent location (Fig. 1A). This prevalent movement pattern did not seem to change with season or time of day and defines the activity space. However, most sharks tracked did undertake brief longer excursions into little used areas. Figure 1B depicts the cumulative activity plots of Shark #35, wherein the usual activity region for this shark (i.e., the southwestern margin of the North Sound) is easily distinguished from two jaunts to the eastern shoreline of the North Sound. Other sharks occupied areas hundreds of meters from shore for varying amounts of time. Figure 1C portrays a magnified view of Figure 1B and shows another characteristic movement pattern of young lemon sharks. In this figure, circles are daytime telemetry fixes, squares are nighttime points, and triangles are twilight locations, demonstrating that there is no diel difference in space usage. Figure 1D shows all MCPs for Shark #23, demonstrating the extreme site attachment exhibited by this shark. All sharks tracked also were site attached.

Figure 1E–F presents exemplary manual tracking segments of Shark #31 which demonstrate the repeatable nature of lemon shark movements. We terminated an overnight track on 4 Aug. 1988 at 0700 h by walking within visual range of this telemetered shark in an effort to evaluate the shark's condition. This attempt at visual diagnosis was habitually made by us at the end of many tracking sessions. At track's end, we observed Shark #31 swimming in a southerly direction within 10 m of marker flag #12. We tracked this individual on five ad-

TABLE 1. SUMMARY OF PARAMETERS OF THE HOME RANGES OF 17 JUVENILE LEMON SHARKS. MCP = Minimum Convex Polygon; ECC = Eccentricity; LI = Linearity Index; IOR = Index of Reuse; AR = Activity Radii; see text.

Shark	Area (km <sup>2</sup> )		Site attachment indices		
	MCP	ECC	LI	IOR	AR (m)
1	0.23	1.0	0.05	22.0	207
3	0.35	7.6	0.29	23.7	1034
7	0.27	8.4	0.02	44.4	425
8	0.55	2.4	0.08	10.1	351
9	0.34	3.1	0.01	11.5	427
14	0.55	3.9	0.06	42.5	529
16	0.78	3.7	0.02	39.0	490
17	0.43	7.9	0.01	39.3	552
18	0.42	3.0	0.02	72.5	412
20	1.21	4.7	0.04	58.2	485
23	0.43	5.8	0.04	42.1	403
24	0.93	2.2	0.01	64.4	540
27	0.88	3.1	0.01	39.6	257
28	1.15	6.5	0.05	34.0	742
31	0.93	2.2	0.01	41.8	475
34	0.78	7.5	0.01	39.6	413
35	1.26	1.3	0.01	57.1	238
Means =	0.68	4.4	0.04	40.1	469

ditional morning twilight sessions over the next 20 days. This shark swam south past marker flag #12 at 0612 h on 7 Aug. 1988, at 0640 h on 8 Aug. 1988, at 0638 h on 13 Aug. 1988 (Fig. 1E), at 0732 h on 22 Aug. 1988 (Fig. 1F), and at 0632 h on 24 Aug. 1988.

*Parameters of home range.*—Error polygons averaged 210 m<sup>2</sup>. Mean dimensions of the home ranges were 2029 m × 569 m. The mean daily shift in COA location was 327 m/d (i.e., about 17% of the mean home range length per day). However, the mean distance between the COAs of the initial and final tracking segments (9–153 days later) was only 56 m.

The observation-area curves of 17 sharks reached an asymptote (with observations varying from 52–162), which allowed for unbiased estimation of the area of their activity spaces. Minimum Convex Polygon (MCP) estimates averaged 0.68 km<sup>2</sup> (range = 0.23–1.26 km<sup>2</sup>). Figure 2 demonstrates the positive correlation between activity space size and shark length (linear regression:  $r^2 = 0.76$ ,  $P < 0.01$ ).

The mean ECC value for the activity spaces of juvenile lemon sharks is 4.4 (range = 1.0–8.4; Table 1), which differs significantly from that of a symmetric home range ( $t = 5.60$ ,  $P < 0.0001$ ).

The three indices of site attachment used

herein are separate and one cannot be predicted from another. We calculated three indices of site attachment (Table 1) to allow greater potential comparison of our results with those of other studies. The mean Linearity Index (LI) was 0.044 ( $n = 17$ ; range = 0.003–0.292), mean Index of Reuse (IOR) = 0.40 (17; 0.10–0.72), and mean Activity Radii (AR) = 496 m (17; 207–1034 m). Mean Index of Reuse (IOR) values between neighboring conspecifics was 0.54 (12; 0.17–0.82).

#### DISCUSSION

Telemetered patterns of movement revealed a generalized space use by juvenile lemon sharks. One important aspect is that the home ranges of most juvenile sharks were narrow expanses very close to shore. Telemetered and nontelemetered sharks were often seen swimming close to the shoreline in such shallow water that their 6-cm high dorsal fins were exposed to air. All sharks typically exhibited laplike movement patterns, characterized by repeated, greatly attenuated, horizontal loops along the shoreline, regardless of the shark's location or time of day. Indices of Eccentricity (mean = 4.4) indicated linearly shaped activity spaces whose ECC values were similar to those published for other near-shore species (e.g., Winter, 1977).

The only exceptions to the above generalization were infrequent (<10% of fixes) long-distance excursions undertaken by telemetered sharks. These jaunts usually resulted in the tracked shark traveling well out of its typical activity space and sometimes into a different habitat (e.g., hundreds of meters away from the mangrove-fringed shoreline into deeper water). Such uncommon movements have been well documented in most classes of telemetered vertebrates (Carey et al., 1990).

A second important aspect of the movements of young lemon sharks is the repeatable nature of activity of individuals. Complexities of patterns of movement, geography, and time of day permitted elucidation of precisely repeated movements in only three sharks. However, we believe that dedicated experimental design and careful data analysis would reveal spatiotemporal repeatability in the majority of juvenile lemon sharks, at least over the short term. The benefit which repeatability of movements affords juvenile lemon sharks is unknown.

A third significant aspect of the movement patterns of juvenile lemon sharks is their persistence in well-defined areas. Telemetered juvenile lemon sharks had direct access to about 50 km of suitable habitat at Bimini, yet they

each used less than 5% of the available shoreline. Such repeatable spatial patterns of movement suggest strong site attachment (McKibben and Nelson, 1986). Similar observations of repeatable behavior have caused other workers to suggest that some sharks are site attached (e.g., McKibben and Nelson, 1986; Gruber et al., 1988; Strong, 1989).

Site fidelity represents a behavioral continuum which spans from nomadism to site attachment (Gruber et al., 1988). We calculated three different indices of site attachment; all three provided evidence that juvenile lemon sharks establish site-specific home ranges. Our calculated LI values (mean = 0.044) indicate considerable revisitation of a preferred area. Similarly, Index of Reuse (IOR) values demonstrated that, each day, juvenile lemon sharks reuse approximately 40% of the previous day's home range. This is well within the range at which animals are considered to be site attached (Cooper, 1978). Finally, site attachment can be inferred from Activity Radii (AR). Mean AR were 496 m (i.e., the average fix was about 500 m from the COA), and >75% of all AR values were less than 584 m. Comparing the mean dimensions of the home ranges of telemetered lemon sharks (i.e., 2029 m  $\times$  569 m) to the above AR values reveals that juvenile lemon sharks typically do not approach the border of their home ranges. In fact, lemon sharks use only about 50% of their home range length. Based on the above indices, we conclude that the home ranges of juvenile lemon sharks are highly site attached.

Animals should establish a home range which is large enough to recover from repeated exploitation of preferred resources. We suggest that juvenile lemon sharks shift foraging sites within their home ranges from day to day, thus effectively allowing neglected areas to recover in their absence. This contention is supported by the above analysis of AR values, IOR values, and the daily shift in COA location. For example, AR values show that only 50% of home range length is used each day. Also, mean IOR values (0.40) indicated that about 60% of the area occupied on day  $t$  was not occupied on day  $t - 1$ . Finally, mean COA drift was 327 m/d, whereas the mean distance between the locations of the initial and final COAs was only 56 m.

A second behavioral continuum, representing site defense, spans from establishment of a completely exclusive territory, through indiscriminate sharing of one's home range, to social behavior between conspecifics. Data on spatial relationships can also be used to evaluate a species' position along this second continuum.

Territoriality, defined as defense of an area (via advertisement or actual exclusion), is an aggressive strategy used by an individual to secure a disproportionate share of any resource with potential significance to its reproductive success (Hamilton et al., 1967; Hutton, 1989). Two criteria are to be satisfied if one is to demonstrate the existence of a territory: (1) individuals must establish home ranges, and (2) potential competitors must be excluded from some portion of this home range (i.e., the "territory"; Brown and Orians, 1970; Myrberg and Thresher, 1974).

We demonstrated that juvenile lemon sharks establish home ranges. Site defense, the second criterion of Brown and Orians (1970), is most likely to occur between conspecifics of the same age due to expected similarity of resource exploitation (Krebs, 1985). Therefore, we calculated IOR values between home ranges of neighboring lemon sharks. Support of criterion #2 could be gained if these interhome range IOR values approached zero, indicating exclusion of conspecifics from an individual's home range. However, adjacent home ranges of lemon sharks overlapped broadly, suggesting that site defense does not occur and that territories, according to the definition by Brown and Orians (1970), do not exist. Our repeated observations of social interactions between juvenile lemon sharks, as described previously for lemon sharks (Gruber et al., 1988), bonnetheads, *Sphyrna tiburo* (Myrberg and Gruber, 1974), scalloped hammerheads, *S. lewini* (Klimley and Nelson, 1981), and gray reef sharks, *Carcharhinus amblyrhynchos* (McKibben and Nelson, 1986), support the view that young lemon sharks are highly social. Telemetered sharks in this study were seen to routinely perform the behaviors "circle-head-to-tail" and "follow" (as described by Myrberg and Gruber, 1974). Also, small aggregations of lemon sharks (approximately 4–7 individuals) often were seen by us to feed simultaneously on isolated schools of bait fish, particularly at dusk.

The present study has demonstrated that area of home range and size of shark are positively correlated. This result supports McNab's (1963) prediction of positive correlation between foraging area and body size. This finding also supports the working hypothesis of Gruber et al. (1988) that area of home range and shark length are positively correlated throughout the shark's ontogeny. For example, juvenile lemon sharks in this study (mean TL = 73.4 cm) occupied a home range with a mean area of 0.68 km<sup>2</sup>. Gruber et al. (1988), using a different experimental design, tracked nine large lemon sharks

and reported home range areas of 18 km<sup>2</sup> for a 168-cm TL shark and 93 km<sup>2</sup> for a 230-cm TL individual. Therefore, home range size in lemon sharks may increase at a rate which is many times greater than the increase in body length, keeping with McNab's (1963) predicted exponential function.

To arrive at a generalization regarding energy accumulation and home range size one must survey a variety of species. Unfortunately, few workers have attempted to examine McNab's (1963) model in an aquatic context; those which have report a variety of results. Todd and Rabeni (1989) radiotracked 34 smallmouth bass, *Micropterus dolomieu*, and did not find a correlation between size of home range and fish length. Similar results were obtained by Miller and Menzel (1986) for muskellunge, by Strong (1989) for horn sharks, *Heterodontus francisci*, and by Fish and Savitz (1983) for four species of freshwater teleosts. However, Fish and Savitz reported a negative correlation between activity space and body size in the bluegill, *Lepomis macrochirus*, whereas Grant and Kramer (1990) pooled published data to demonstrate that body length explained 87% of the variation in size of the home ranges of salmonids. We attempted to determine whether a general correlation exists between body size and home range area in fishes by surveying 74 published estimates of home range area of different species. Our survey failed to reveal any correlation, perhaps due to the large variation of methodologies used in those studies (Swihart and Slade, 1985; Worton, 1987).

Because telemetered specimens are studied for the purpose of extrapolation to untagged individuals (Ross and McCormick, 1981), it is important to consider the extent to which results are biased by the effects of the telemetry package (Ormiston, 1985). We believe the intracoelomic transmitters used in this study had negligible effects on the results presented here because of the following: (1) Telemetered sharks seemed to exhibit normal behavior, swimming ability, and physical appearance. (2) In all cases, they successfully competed with intact captive sharks in the same pen for food, which we offered them, and fed soon after surgery. (3) Studies have shown that a transmitter will not cause negative effects if its weight in air is less than 2% of the fish's body weight (e.g., Mellas and Haynes, 1985). Our transmitters were about 1.75% of the smallest telemetered shark's body weight. (4) Telemetered sharks that were recaptured grew at rates which were not significantly different than those tagged with tiny, injectable tags (C. A. Manire and S. H. Gruber,

unpubl. data;  $t = 0.521$ ,  $P > 0.5$ ). (5) During many tracking sessions, both telemetered and nontelemetered sharks swam close to and even under the tracking craft, or even occasionally stopped within a few meters of the tracker. In summary, telemetered sharks exhibited normal appearance, grew at normal rates, and survived for at least 1055 days after surgery. Therefore, the surgical procedure, presence of the transmitter, and/or presence of the tracker did not seem to affect these sharks.

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