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Seasonality of calving and predation risk in bottlenose dolphins on Little Bahama Bank

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Most studies of seasonal reproduction in odontocetes have considered bottom-up forcing through seasonal changes in the physical environment and/or prey availability (Wells *et al.* 1987, Read 1990, Urian *et al.* 1996, Mann *et al.* 2000, McGuire and Aliaga-Rossel 2007, Westgate and Read 2007), which are typically more pronounced

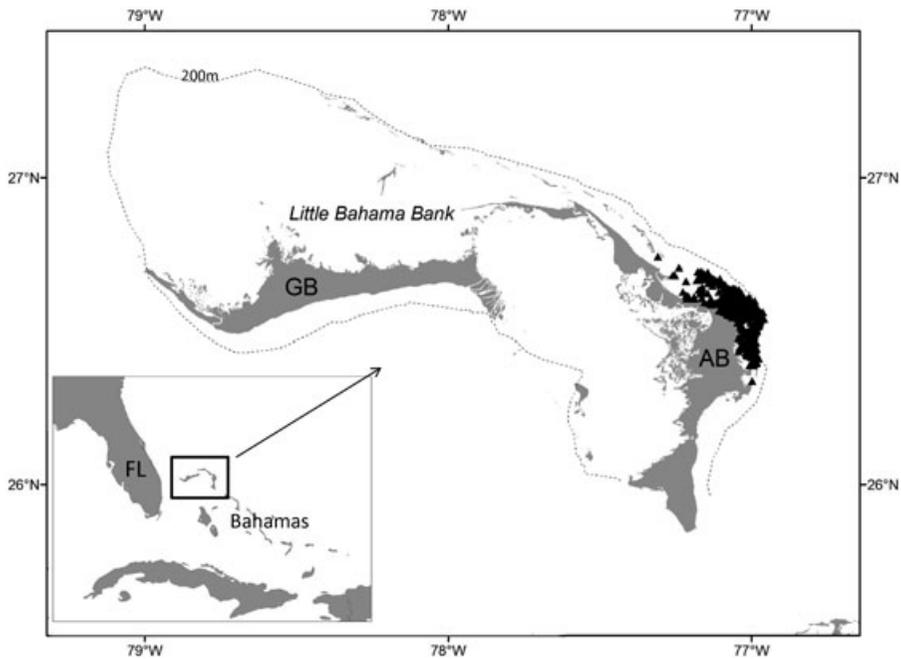


Figure 1. Map of Little Bahama Bank, around Abaco Bahama (AB) and Grand Bahama (GB) Islands. The bank is surrounded by the deep waters of the NW Atlantic Ocean, with the 200 m depth contour represented by a broken line. Locations of 788 dolphin encounters between 1992 and 2007 are represented by solid triangles off the east side of Abaco Island where surveys were conducted. The insert shows the position of the study area in the northern Bahamas off the east coast of Florida (FL).

in high latitudes. In contrast, there has been little consideration of top-down selection through seasonal changes in predation pressure. Predation pressure by sharks has been shown to affect delphinid habitat use and group size (Norris and Dohl 1980, Wells *et al.* 1987, Heithaus 2001, Heithaus and Dill 2002), but the influence of predation pressure on reproductive patterns of dolphin populations has rarely been assessed. Here, we report on a distinct seasonal peak in calving for bottlenose dolphins (*Tursiops truncatus*) using Little Bahama Bank, despite its tropical latitude and describe an inverse seasonal peak in the risk of predation by sharks, inferred by the incidence of fresh shark-bite wounds (Heithaus 2001). We suggest seasonal changes in the environment that might mediate increased predation risk and hypothesize that this may be a selective force for calving seasonality.

Little Bahama Bank ($\sim 26^{\circ}\text{N}$, $\sim 77^{\circ}\text{W}$) comprises part of the northern Bahamas and encompasses the two main islands of Great Abaco and Grand Bahama (Fig. 1). This carbonate bank is approximately $17,000\text{ km}^2$ in size (approximately 65% covered by water), characterized by shallow waters (average $<7\text{ m}$ deep) and chains of small islands, and is bounded on all sides by the deep ($>500\text{ m}$) waters of the subtropical NW Atlantic Ocean. Approximately 1,000 bottlenose dolphins inhabit the bank (Durban 2002), and individuals from this inshore dolphin population have not been sighted in the surrounding pelagic waters, despite extensive survey effort over

Table 1. Total number of dolphins and neonates identified and the number of individuals with fresh shark-bite wounds for each month pooled over all years (1992–2007). Also presented are the total number of dolphin groups encountered in each month, and the number of years in which each month was surveyed. Water temperature data are also presented by month for March 2007 to February 2008, recorded at a coastal mangrove creek within the study area,¹ along with the average surface water temperature during dolphin encounters (1992–2007), where available. Tropical cyclone seasonality is indicated (***) based on long-term records reported in Landsea (1993), along with named storms whose centers passed within 60 nm of the study site during the 1992–2007 study period (<http://www.hurricanecity.com/city/abacoisland.htm>).

Month	Years surveyed	Groups encountered	Total IDs	Neonates	Fresh wounds	Water temperature °C (at dolphins)	Cyclone season (Abaco storms)
January	10	43	67	3	0	22.5 (NA)	–
February	8	58	76	4	1	24.4 (23.6)	–
March	9	63	95	1	0	23.1 (22.3)	–
April	8	39	77	0	0	25.1 (22.8)	–
May	5	27	31	0	0	26.5 (NA)	–
June	9	85	85	0	0	28.6 (27.4)	***
July	7	56	76	0	2	31.1 (29.2)	*** (Bertha 1996)
August	6	65	76	0	4	31.0 (28.2)	*** (Erin 1995 ^a), (Dennis 1999)
September	2	123	83	0	4	29.8 (28.4)	*** (Floyd 1999), (Frances 2004 ^a), (Jeanne 2004 ^a)
October	9	138	107	0	3	28.0 (27.2)	***
November	8	54	79	3	0	24.3 (26.2)	–
December	5	48	55	5	2	24.3 (NA)	–

¹Unpublished data from Craig Layman, Florida International University, 3000 NE 151st Street, North Miami, FL 33181.

^aNo field effort was conducted in the 2 mo directly following each of these hurricanes.

more than 16 yr, and therefore, this population appears to be restricted to this shallow bank system (Parsons *et al.* 2006). Seasonal variability in surface water temperature on Little Bahama Bank is limited, but temperatures are moderately elevated in summer compared to winter (Table 1). This increase in summer temperatures is coincident with tropical cyclones in the NW Atlantic (Vecchi and Soden 2007), which typically occur between June and October (Landsea 1993). To examine seasonal differences, we defined a 6 mo “summer” period (May–October), characterized by increased water temperatures and encompassing the entire season of tropical cyclones, and a 6 mo “winter” period (November–April), characterized by cooler water temperatures and a complete absence of cyclonic activity (Table 1).

Part of this population has been monitored annually since 1992 through boat-based photo-identification surveys in a 160 km² study site on the east side of Abaco Island (~26°33'N, ~77°04'W; Fig. 1). A total of 251 distinctly marked individual dolphins were identified from 788 different dolphin groups encountered in this study area between 1992 and 2007, based on high-quality photographs (photographic processing methods described in Durban *et al.* 2000). Although surveys were not conducted year round in every year of the study, the population was surveyed in

every month, when pooled across years. The median number of individual dolphins encountered each month, pooled over all years, was 77 (minimum 31, maximum 107) (Table 1). The level of coverage was consistent across seasons, with 185 different individuals documented in “summer” (from 1,665 dolphin identifications) and 175 in “winter” (1,236 identifications).

All encounter photographs were examined to detect newborn dolphins. Neonates were easily distinguished based on small body size (typically less than one-third the size of the mother), dark coloration, and floppy dorsal fin and were often observed surfacing in echelon position next to an attendant adult. However, to standardize for age in this analysis, we designated a calf to be a neonate only when there was clear evidence of changes in pigment around linear “folds” oriented dorsoventrally on the body, resulting from folding of the fetus *in utero*. Sixteen neonates were identified during the 16 yr study, and seven of these neonates were repeatedly identified throughout the year following first sighting. Photographic analysis revealed that fetal folds were typically only evident for approximately 1 mo in this warm-water environment, compared to a period of several months and even years in bottlenose dolphins from more temperate habitats (Grellier 2000) and therefore provided a reliable indicator of recent birth.

All encounter photographs were also examined to document fresh shark-bite wounds on individuals. Fresh wounds do not, of course, inform us of mortality events as a result of predation, but we assume that they provide an indicator of predation pressure. Wounds were classified as shark bites based on a semicircular shape matching a shark’s jaw and marks resembling teeth marks were observed in association with most large wounds. Additionally, fresh wounds were identified based on a dark tone (black and white images) or red color (digital images) from exposed blood or muscle (Corkeron *et al.* 1987*a, b*; Orams and Deakin 1997; Heithaus 2001). Sixteen fresh shark-bite wounds were identified in total, comprising adult males (2), adult females (3), adults of unknown gender (3), subadults (2), and juveniles (6). Although constrained by small sample size, this relatively high proportion of juveniles with fresh wounds might imply the targeting of young animals by predatory sharks, and we note also that all three adult females with fresh wounds had dependent calves at the time. Analysis of within-year resightings, possible for nine of these dolphins, documented that these wounds only appear fresh (red or dark) for typically around a month, and therefore, we consider fresh wounds to be a sensitive indicator of the timing of shark attacks. Similar healing rates were reported in another warm-water study area off Australia (Corkeron *et al.* 1987*a*, Orams and Deakin 1997), where the complete closure of a fresh shark-bite wound was observed to occur within 30 d and all that remained after 45 d was “an obvious indented white un-pigmented scar” (Orams and Deakin 1997). Wounds from skin and blubber biopsies from dolphins in our Abaco study site were also reported to be “closed” (covered by epidermal tissue) after 30 d (Parsons *et al.* 2003).

To assess monthly variability in both calving and shark bite wounding rates, data across 16 yr (1992–2007) were pooled into 12 calendar months to count both the number of neonates and individuals with fresh shark-bite wounds in each monthly interval. To control for survey effort, and the degree to which the population was sampled, the number of neonates/newly wounded individuals was represented as a proportion of the total number of individuals identified in each month, pooled across all years. Because the sample sizes of both neonates and newly wounded dolphins were low, and the total number of identifications varied across the months, point estimates of proportions will vary in how well they represent the true proportion of calves/newly

wounded dolphins in the population. To account for inherent uncertainty in these estimates of proportions, we adopted a Bayesian model for the estimation of the proportions, to represent uncertainty in the form of probability distributions (Gelman *et al.* 1995). The number of neonates/individuals with fresh wounds in each month was modeled as binomially distributed from the total number of individuals identified in that month. This allowed the binomial proportions to represent an estimate of the proportion of individuals that were neonates/newly wounded. Each monthly binomial proportion was initially assigned a flat prior distribution between 0 and 1, which was updated, conditional on the data to estimate the posterior distribution for each monthly proportion. We used the WinBUGS software (Lunn *et al.* 2000) to implement Markov Chain Monte Carlo (MCMC) sampling to simulate sequences of values from the posterior distributions conditional on the observed data. The sampled values were then used to construct box plots of the posterior distributions for parameters of interest and estimate summary statistics for the posterior distributions.

To examine seasonal differences, we modified our Bayesian model to have a separate probability distribution underlying the proportions of calves/individuals with new wounds in both winter and summer. In particular, instead of a separate prior distribution for each month, we adopted a separate flat prior probability distribution for each season. When the estimates for the two seasonal distributions were made in the same MCMC run, we calculated the proportion of the MCMC sampled values, where the winter proportion of calves/wounds exceeded that from the summer (or *vice versa*), providing an estimate of the probability that the proportions were higher in one season than the other, while accounting for the variability in each seasonal distribution.

Despite uncertainty due to sample sizes (see error bars), there were clear differences across months in the proportion of individuals that were new calves (Fig. 2), with neonates only identified during the “winter” months. The calving rate peaked in December, with a posterior median for the proportion of individuals that were neonates of 0.10 (95% Probability Interval [PI] = 0.04–0.19) and was lowest in October (posterior median = 0.01, 95% PI = 0.00–0.03) (Fig. 2). Notably, almost all calves (15/16 or 94%) were born during 4 mo (November–February) of the winter period. As a result, there was marked difference in the monthly average calf proportion between seasons. The calf proportion in winter (posterior median = 0.09, 95% PI = 0.06–0.14) was significantly greater than that in the summer period (posterior median = 0.003, 95% PI = 0.00–0.02), with no overlap of the posterior distributions and therefore a high probability ($P = 1$) that the summer and winter calf proportions were different.

Most (13/16, 81%) of the shark-bite wounds we observed were acquired during a 4 mo period (July–October) within the summer season for tropical cyclones and increased water temperatures. The wounded proportion was highest in both August and September, with a posterior median for the proportion of individuals that possessed fresh wounds of 0.06 (95% PI = 0.02–0.13 and 0.02–0.12, respectively) and was lowest in March (posterior median = 0.01, 95% PI = 0.00–0.04; Fig. 3). The wounded proportion was significantly higher in summer (posterior median = 0.07, 95% PI = 0.04–0.12) compared to winter (posterior median = 0.02, 95% PI = 0.01–0.05). There was some overlap in the ranges of posterior distributions for these two estimates, but little overlap in the regions of highest probability density, and therefore, a very high probability ($P = 0.99$) that the summer and winter average wound proportions were different. Notably, the majority (11/16) of the documented wounds were observed immediately following either the direct passage of hurricane

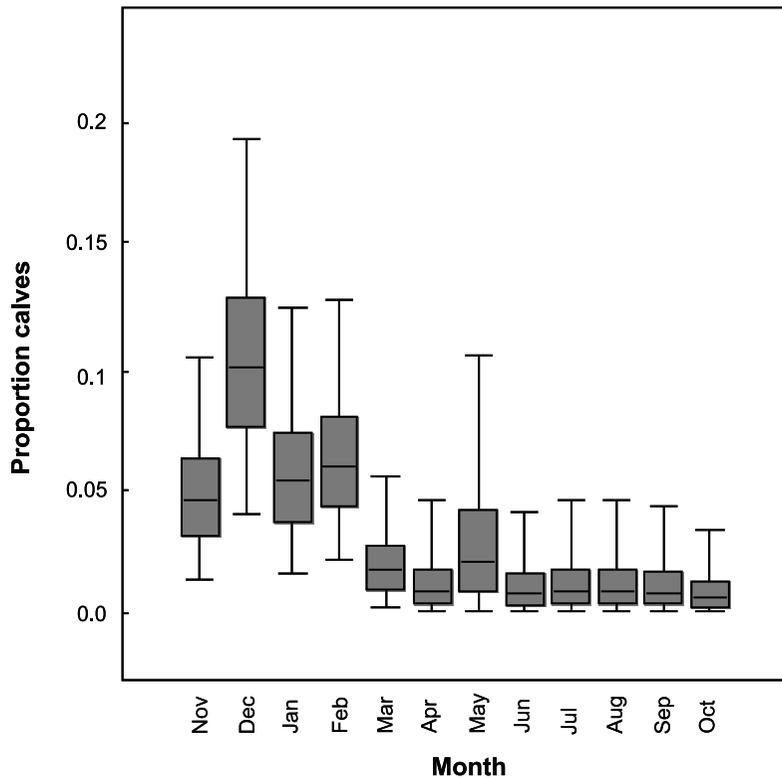


Figure 2. Box plot of the number of neonates as a proportion of the total number of individuals identified in each month. Vertical lines represent the intervals encompassing 95% of the distribution, the boxes represent the central 75% interquartile range, and horizontal lines represent the posterior medians.

Bertha over Little Bahama Bank in July 1996 or the joint impact of direct hits from Hurricanes Dennis and Floyd in late August and September 1999.

These data describe distinct calving seasonality for dolphins on Little Bahama Bank, with all neonates documented during the winter months and none documented during the 7 mo with the highest water temperatures. This is similar to findings from higher latitude study sites, where distinct calving seasonality of odontocetes has been suggested to be linked to seasonal changes in water temperature and/or changes in prey (Read 1990, Urian *et al.* 1996, Haase and Schneider 2001, Thayer *et al.* 2003, Westgate and Read 2007). However, there are notable contrasts with these studies, as calving in our study is inversely related to summer increases in water temperature, and the temperature variability on Little Bahama Bank is relatively minor compared to higher latitudes.

We cannot rule out the possibility of calving in response to a seasonal shift in prey availability, as we do not have detailed data on feeding habits. It is also possible that even small increases in water temperature in this shallow water system create an environment that is too physiologically demanding in summer. High costs of maintaining a stable body temperature, when confronted with suboptimal ambient

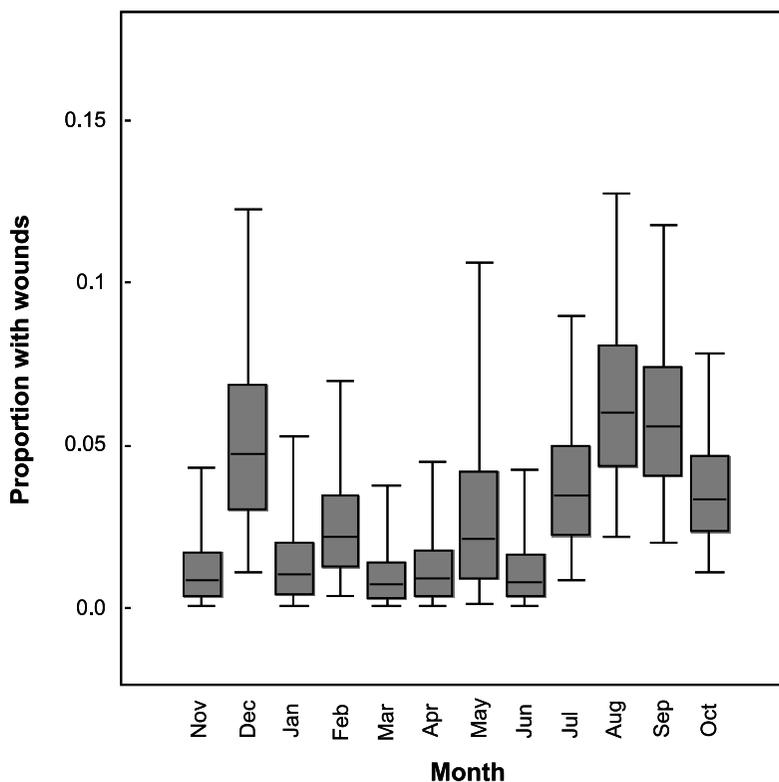


Figure 3. Box plot of the number of individuals with fresh shark-bite wounds as a proportion of the total number of individuals identified in each month. Vertical lines represent the intervals encompassing 95% of the distribution, the boxes represent the central 75% interquartile range, and horizontal lines represent the posterior medians.

temperatures (high or low), have been shown to lead to changes in reproduction and survival of several mammalian populations (Ohsawa and Dunbar 1984, Rutberg 1987, Dunbar 1990, Boyd 1996, Hill *et al.* 2000). However, the inverse correlation between calving seasonality and the acquisition of fresh shark-bite wounds suggest that seasonal changes in the environment may have also selected indirectly for calving seasonality by driving shifts in distribution and habitat use of dolphins and/or predatory sharks that have increased predation risk.

Unfortunately, data on shark movements is lacking from our study area, and equal-area coverage surveys for dolphins have not been conducted year round to provide a robust assessment of changes in dolphin distribution. Nonetheless, 13 of 16 fresh shark-bite wounds on dolphins were documented in the summer months, indicating a seasonal change in dolphin and shark interactions. We suggest that dolphins seeking cooler oceanic waters, or alternate prey sources, may spend more time in summer close to the deeper, exposed waters at the edge of the bank, which in turn may expose them to increased predation risk from oceanic sharks, particularly tiger sharks, that are known to prey on dolphins (Corkeron *et al.* 1987*a, b*; Cockcroft *et al.* 1989; Cockcroft 1991; Heithaus 2001). There may also be seasonal inshore

movements of sharks, but although predatory sharks are common in the deep waters surrounding Little Bahama Bank, they are rarely sighted in the shallow, protected waters on the bank.¹

The selective disadvantage of calving in summer may be accentuated by acute weather events, specifically the incidence of hurricanes. Hurricanes are a key feature of climatic and seasonal variability in the environment of the NW Atlantic (Landsea 1993, Webster *et al.* 2005, Vecchi and Soden 2007). These storms have been shown to have significant impact on both marine and terrestrial ecosystems (Spiller *et al.* 1998, Walther *et al.* 2002, Harley *et al.* 2006) and have been implicated in the mass stranding of cetaceans (Mignucci-Giannoni *et al.* 2000). The wind-driven wave heights and storm surge during intense hurricanes easily exceed the shallow water depth on Little Bahama Bank, making the shallow waters uninhabitable to dolphins. Although we have one anecdotal report of dolphins in a protected creek during Hurricane Bertha in 1996, we suspect that the primary survival response is to seek this deeper water habitat at the edge of the bank, which in turn exposes them to increased predation risk from oceanic sharks. Most (11/16) of the fresh shark-bite wounds were documented immediately following either the direct passage of Hurricane Bertha over Little Bahama Bank in July 1996 or the joint impact of direct hits from Hurricanes Dennis and Floyd in late August and September 1999. Unfortunately, photo-identification effort was limited in the months immediately following hurricanes in recent years. Nonetheless, these data suggest that predation risk is increased by these acute weather events. Notably, all neonates documented during this study were outside of the hurricane season for the NW Atlantic (June–October, Landsea 1993), and only two calves were documented in the three calendar months prior to the onset of hurricane season. We suggest that this may be a response to the selective disadvantage of rearing a young calf during this potentially dangerous time (Miller *et al.* 2010).

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