Jaguar (*Panthera onca*) Predation of Sea Turtles (*Chelonia mydas, Eretmochelys imbricata, and Dermochelys coriacea*) at Tortuguero National Park, Costa Rica

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Abstract

Jaguars have been recorded as utilizing sea turtles as a seasonal food source. However, the exact nature of their predator-prey relationship has not been thoroughly studied. In order to gain a better understanding of this relationship, this study was developed with several objectives in mind, all looking at the spatiotemporal patterns of jaguar predation on sea turtles. It was hypothesized that there would be no correlation between jaguar activity and turtle activity (H_0: r = 0).

The study was conducted at Tortuguero National Park, Costa Rica. Infrared cameras were placed at strategic locations where photos and video would be taken of jaguars in order to identify specific individuals based on their unique markings. By identifying the number of individuals captured and recaptured, the density of the jaguar population could be estimated. Along the shoreline, from mile marker 17.5 to mile marker 3, a weekly survey was conducted to examine turtle carcasses. Various data was recorded for each turtle including date, identification number, species, nearest northern mile marker (NNMM), GPS coordinates and accuracy, vertical position, whether the turtle was lying on its front or back, curved carapace length (CCL), parts eaten (if feasible), point of attack (if feasible), and days since kill. On this same survey, both green and leatherback turtle track frequency were recorded. Tracks included both half-moon (no nesting, turtle came up the beach and turned around in "half-moon" arc) and full (turtle came more than half way up the beach, nesting). Also, jaguar track data was recorded. Every half mile, presence or absence of jaguar tracks was noted. Besides presence, the number of entry and exit points of jaguar tracks onto/off of the beach was logged as well as their GPS coordinates. Most of the data was recorded over an eleven month time period, with the exception of entry/exit point data (twenty-three months) and leatherback track data (four months). The jaguar camera data indicated that there were five individuals captured on camera, four of them being recaptured at another time. Some of the data was statistically analyzed using the Pearson correlation coefficient. The r values resulting from this calculation showed that; (1) there is a significant positive correlation between the number of entry/exit points in an area and the number of turtle carcasses found ($r = 0.724$; $p < 0.05$); (2) there is a significant positive correlation between the number of green turtle half-moon tracks in an area where there was also a high frequency of jaguar tracks and exit/entry points ($r = 0.921$; $p < 0.05$); (3) there is a significant negative correlation between the number of green turtle full tracks in an area and the frequency of jaguar tracks and exit/entry points ($r = -0.897$; $p < 0.05$); (4) that there is a significant positive correlation between the number of leatherback half-moon tracks in an area where there was also a high frequency of jaguar tracks and exit/entry points ($r = 0.765$; $p < 0.05$); and (5) there is a significant negative correlation between the number of Leatherback full tracks in an area and the frequency of jaguar tracks and exit/entry points ($r = -0.819$; $p < 0.05$). This study seems to show that jaguar activity/presence may be influencing the behavior of the turtles during the nesting season and their choice of nest site locations. Also, human traffic may be impacting both the jaguars' and turtles' behavior. This has important conservation implications, such as whether jaguars should be provided with an alternative food source.

Keywords: jaguar, sea turtles, predator-prey relationship, predation

Jaguar (*Panthera onca*) Predation of Sea Turtles (*Chelonia mydas, Eretmochelys imbricata, and Dermochelys coriacea*) at Tortuguero National Park, Costa Rica

Since the first instance of a cell consuming another cell, there has been predator-prey interaction. Predators must expend energy hunting for prey, while prey tries to balance energy spent avoiding predators and searching for food for themselves. The question of food supply is what structures and determines the activities of an animal community (Stolzenburg, 2008). The complex interaction between a predator and prey can have many ramifications for the entire ecosystem. For example, it is still debated whether the amount of prey regulates the amount of predators, or whether the amount of predators regulates the amount of prey (Stolzenburg, 2008). Fluctuations in both populations reflect how tied to one another these animals truly are.

In order to be more successful at catching and consuming prey, predator morphology and behavior may change over time. Predators may develop a keener sense of hearing in order to hear small, underground prey. They may change their behavior so that they only come out at certain types of day when their prey is least likely to see them. At the same time, prey species are also changing both physically and behaviorally. For example, in order to avoid being eaten by predators, a prey species may develop some type of body armor. They may also change what time of day they come out so as to avoid times when predators are most prevalent. This constant change and adaptation between a predator and its prey species has been referred to as an “arms race” (Stolzenburg, 2008, p. 36).

Predator-prey interactions occur in the relationship between jaguars and sea turtles. Jaguars are large, solitary predators, with the exception of when a mother has cubs (Eisenberg, 1989). They inhabit a variety of habitats, forests, savannas, scrub land and deserts ranging from Mexico to Northern Argentina (Kitchener, 1991). Several sources describe them as being opportunistic when feeding and having flexible diets (Carrillo, Fuller, & Saenz, 2009; Da Silveira, Ramalho, Thorbjarnarson, & Magnusson, 2010; McBride, Giordano, & Ballard, 2010). Studies indicate that the amount of each species that composes a jaguar's diet is mirrored by the density of each prey species in an area and that the majority of their diet was comprised of mammals (de Oliveira, 2002; Kitchener, 1991). However, Chelonians (a specific family of turtles) were also preyed upon (de Oliveira, 2002).

As early as 1963, it was noted by Louis Autar that jaguars were preying upon marine turtles (Autar, 1994). He found several carcasses of both green (*Chelonia mydas)* and leatherback (*Dermochelys coriacea)* turtles killed by jaguars. Over the next ten years, he kept track of all the dead turtles found, noting that most of these were green Turtles.

One study that reports chelonians in the diet of jaguars was done by Carrillo, Fuller and Saenz (2009). In Corcovado National Park, Costa Rica, scientists looked at jaguar hunting activity. Olive ridley, the most common nesting turtle found at Corcovado, and Pacific green turtles were found preyed upon by jaguars or in their scat. Another study by Silveira, Ramalho, Thorbjarnarson, and Magnusson (2010) on jaguar diet indicated jaguars preyed on seven different chelonian species, deeming them a significant part of the jaguar's diet.

Specifically at Tortuguero National Park, Costa Rica, it has been documented that jaguars prey on marine turtles. In the 1980's, two turtles were recorded as being killed by jaguars (Harrison, Troëng, & Fletcher, 2005). Only in 1997 did larger amounts of turtles begin to be preyed upon (Harrison et al., 2005). From 1997 to 1999, 51 turtles were killed, all green turtles except for two leatherbacks (Troëng, 2000). From 2000-2004, a minimum of 28-97 green turtles were killed each year (Harrison et al., 2005).

The green turtle, which compromised the bulk of the predated turtles, is a sea turtle belonging to the Chelonidae family. All sea turtles are extremely vulnerable to predation when nesting on land. This species has many nesting beaches, with Costa Rica being listed as one of the preferred sites (Bonin et al., 2006). The female comes onto the beach at night during the high tide to lay her eggs (Bonin et al., 2006). She will choose a place among or close to the vegetation. A single clutch usually contains about 100 eggs and one female may lay up to six clutches per season (every 15 days; Bonin et al., 2006). The entire process of nesting takes anywhere from an hour to an hour and a half (Bonin et al., 2006).

The leatherback turtle, another species of turtle found predated upon, is the largest species of sea turtle that nests at Tortuguero. This turtle has an entirely unique carapace or pseudocarapace (Bonin et al., 2006). This pseudocarapace is made up of many “small bones that overlie a thick layer of oily connective tissue and were covered externally by a thin, smooth skin resembling leather” (Bonin et al., 2006, p.198). These turtles return to their natal beaches to nest by night during the high tide (Bonin et al., 2006). The turtle may be fertilized twice and can lay around ten nests every 10-15 days per season (Bonin et al., 2006). Each nest usually contains between 100 to 150 eggs (Bonin et al., 2006). The nesting process can take anywhere from 1.5 to 2 hours (Bonin et al., 2006). While laying their eggs, the turtles go into a sort of trance like state where they were oblivious to their surrounding and any disturbances (Bonin et al., 2006). Costa Rica is listed as one of the current best nesting sites for these turtles (Bonin et al., 2006).

A final species of sea turtle that has been found to be preyed upon at Tortuguero is the hawksbill (*Eretmochelys imbricata*). This turtle nests on tropical and subtropical beaches (Bonin et al., 2006). The female will come up onto the beach, by day or night, and choose a place to nest among the vegetation (Bonin et al., 2006). She can lay anywhere from 50-200 eggs per clutch and can nest 3 or 4 times per season (Bonin et al., 2006). Nesting takes about one hour (Bonin et al., 2006).

Not only has it been observed that jaguars prey upon turtles, but how they do so has been researched a bit as well. Troëng (2000) noted that jaguars usually kill their prey by crushing the skull or neck with their extremely powerful jaws. He also described how the jaguars usually only consume the neck region and occasionally the flippers (Troëng, 2000). A study done in Peru by Emmons (1989) recorded how jaguars broke through the carapace of each turtle species the researcher found preyed upon. Each species had been consumed using different methods of getting through, or around, the carapace.

Although jaguars do indeed utilize sea turtles as a food source, the exact nature of the predator-prey relationship has not been extensively researched. In order to gain a better understanding of this relationship, this study was developed with several objectives in mind: (1) to determine how many jaguars were currently active in the research site using camera traps; (2) to observe how both green and leatherback turtles were utilizing the beach by recording tracks; (3) to examine how jaguars were utilizing the beach by recording presence of tracks and entry/exit points; (4) to see if jaguar activity had any connection to the time of year; (5) to determine if carcass placement had anything to do with the location; (6) to investigate how predation compared to the time of year; (7) to ascertain if there was a relationship between the time of year and turtle activity; (8) to observe how jaguars were killing and consuming turtles; (9) to see if there was any correlation between jaguar activity and turtle activity; and (10) to see if there was any correlation between jaguar activity and frequency of predation. It was hypothesized that there would be no correlation between jaguar activity and turtle activity (H_0: r = 0).

Methods

Research Site

Tortuguero National Park is located along the north-east coast of Costa Rica, bordering the Caribbean Sea. The park was created in 1975 and contains 77,032 acres of land (Costa Rica national parks, 2009). The park contains eleven different habitats including high rainforest and herbaceous lagoon (Costa Rica national parks, 2009). This area receives abundant rainfall (240in per year) making it abundant in waterways (Costa Rica national parks, 2009).

The south end of the park is the Jalova River mouth. This area used to be a lagoon and the river was cut off from the sea. In more recent times, erosion and currents have opened the river mouth, making it an estuary. The north end of the park is bordered by the small town of Tortuguero.

Tortuguero National Park is most famous for its beaches where marine turtles come to nest. Tortuguero in Spanish means, “place of the turtles” (Troëng, & Rankin, 2004, p. 111). It is reported that green, hawksbill, loggerhead (extremely rare) and leatherback turtles all nest at Tortuguero (Costa Rica national parks, 2009). This beach is the largest green turtle rookery in the Atlantic basin and one of the two largest in the entire world (Troëng & Rankin, 2004).

Camera Traps

In order to establish the proper method of camera trapping and then interpreting the results, the methods and conclusions of Gomez and Ayala (2004) were examined. From their study, a protocol was determined. The data for the camera portion of the study took place over a nine month time period.

Cameras were set up along the (1) North trail at miles 15 and 17, (2) the beach access trails off of the North trail at miles 16.5 and 16, and (3) near recently killed turtles that were found. Sites were chosen based on previous jaguar sightings, presence of jaguar tracks, or presence of recently predated turtles. The cameras that were used were customized Gobblecams and 2010 Bushnell Trophycams.

Humidity/moisture absorbers were also placed in the camera boxes so the cameras did not become too damp. These camouflaged boxes were then strapped to trees 30-60 cm above the ground and then locked in place with a cable and padlock to deter theft. Ideally, two cameras should be placed at the same site, one on either side of the trail (though not directly across from one another). This ensures that both sides of the animal are recorded to help positively identify the individual. The cameras either took pictures or recorded short segments of video, based upon the setting. Photos/video were recorded when the passive infrared motion sensor detected either motion or body heat. Cameras were not set up in areas with high human traffic.

Cameras were checked at least once per week. Cameras were removed and placed at different locations based on the decision of the site manager. A notebook was kept for recording data about the camera traps. When a new site was chosen and a camera was placed, a team member recorded the: date; the team members' initials; the site number; camera number; the nearest northern mile marker; the GPS coordinates; and a physical description of the site such as the vegetation on which the camera was placed. When a team changed the batteries, removed a memory card and replaced it, or just checked on the camera for problems, data was again recorded. This data includes: date; team members' initials; site number; camera number; action taken; and any problems/other relevant information.

Memory cards were periodically checked for photos/footage. All photos were kept and sorted into categories. Categories included: nothing in photo; jaguars; prey species; other. All jaguar photos/video were analyzed to identify individuals. To identify an individual, markings on both sides were looked at and unique patterns were recorded.

Jaguar Predation

The survey was conducted on the shoreline located in Tortuguero National Park, Costa Rica. The survey began at Mile 18 (N10° 21' 22.3", W83° 23' 28.7") and ended at Mile 3.5 (N10° 32' 13.1", W83° 29' 57.6"). This covered a stretch of beach 14.5 miles in length.

Several pieces of data were collected. One of these was turtle track data. Every 0.5 miles, the number of full and half-moon turtle tracks in the previous 0.5 mile was recorded. A full track was defined as when a turtle went more than half-way up the beach and nested, while a half-moon was defined as when a turtle came up the beach and turned around in "half-moon" arc without nesting. Green track data was collected over a time period of eleven months while leatherback track data was collected over a period of four months. Though hawksbill turtles did nest at Tortuguero and were included in the carcass count, their tracks were not recorded since their frequency was so rare.

Every 0.5 miles, the presence or absence of fresh (determined by individual and occasionally verified by team) jaguar tracks in the previous 0.5 mile stretch was also recorded. If there were no fresh tracks present, a 0 was recorded. If fresh tracks were present, a 1 was recorded. This data was collected over an eleven month period. Entry and exit points of jaguar tracks on/off the beach were also noted. Unlike track presence data, this data was recorded over a twenty-three month period of time. Entry points were where jaguar prints were seen emerging from the vegetation and coming onto the beach. Exit points were defined as the opposite of this. At either an entry or exit point, GPS coordinates of that location were recorded.

The largest chunk of data recorded dealt with dead turtles. Surveys to record turtle carcass data occurred once per week over a time period of eleven months. A dead turtle was only recorded if it has not been recorded on a previous survey. For turtles that were new, or that have not been previously recorded, the following data was collected: date; identification number; species; nearest northern mile marker (NNMM); GPS coordinates and accuracy; vertical position; whether the turtle was lying on its front or back; curved carapace length (CCL); parts eaten (if feasible); point of attack (if feasible); days since kill; and comments were noted. Vertical position regards where the turtle was located on the beach and how much sun reaches the carcass. The letter "V" indicates vegetation where no/little direct sunlight touches. The letter "B" indicates border in which the area receives direct sunlight at parts of the day. An "O" indicates open where direct sunlight hits most of the day. Curved carapace length is measured differently depending upon the species of the turtle. For green and hawksbill turtles, the “CCL” was taken down the center of the carapace with a 150cm measuring tape. The 0 end was placed at the nuchal scute (where the neck skin touches the carapace) and measured to the posterior notch in the carapace. For leatherback turtles, the CCL was taken down alongside the middle longitudinal keel using a 300cm measuring tape. The “0” end was placed where the neck skin meets the shell (no scutes) and follows to the side of the midline, or center, longitudinal keel down to the tip of the peduncle/caudal projection. To determine the number of days since the carcass was killed, it was examined for certain characteristics as outlined in the Appendix. After these features were examined, the researcher placed the kill time in one of several categories: 1-2 days; 2-4 days; 4-7 days; 7-14 days; 14-21 days; and 21+ days. This would allow us to see when the jaguars were preying on the highest number of turtles. Besides recording data, two photographs, minimum, were taken. One was a close-up of the turtle including the identification plate (which showed date and turtle ID) and any significant features. This photo encompassed the entire turtle. The other photo was a landscape taken of the turtle, with the photographer’s back to the sea. The photo included the identification plate as well as any key features of the landscape that would give an indication of where it was located and the conditions there. The turtle was not moved to make these photographs possible.

Statistical Analysis

When analyzing whether or not two variables were related, several statistical methods can be used. One of the most common is the Pearson correlation coefficient. The correlation coefficient (r) determines whether there was a positive or negative association between the different variables (e.g. presence of jaguar tracks and turtle tracks). The correlation coefficient can be anywhere from -1 to +1 (Jackson, 2012). The closer the r value is to +1, the stronger and more positive the correlation between the two variables (Setchi et al., 2010). This means that as one variable increases or decreases, so does the other. The closer the r value is to -1, the stronger the negative correlation between the two variables is (Setchi et al., 2010). This relationship means that as one variable increases, the other decrease or vice versa. An r value of 0 would indicate that there is no relationship between the two variables and perhaps a different test should be used (Setchi et al., 2010). It must be noted that this statistical test does not look at significance, but rather correlation. Significance was determined using an alpha scale of $p < 0.05$.

Results

Jaguar Camera Trapping

Over the course of 251 trapping days, 89 cameras were set up. These cameras captured a total of 154 photos that included jaguars (Table 1). These photos were used to identify specific markings on the jaguars (Fig. 1). From these identifications, it was determined that as many as five adult jaguars had been captured on camera. Four of these have been “recaptured” on camera. Also, four videos of jaguars were taken with the cameras as well.

Table 1. Jaguar camera data. This table shows the periods of time these cameras were set up in. The number of trapping days indicates the total number of days cameras were capturing photos/videos. The number of cameras refers to the number of camera sites set up on trails. The table also shows the number of pictures and videos taken specifically of jaguars which were used to identify the number of jaguars in the area.

Phase #/Date	Number of Trapping Days	Number of Cameras	Number of Jaguar Pictures	Number of Jaguar Videos	Number of Jaguars Identified
104 Oct-Dec	14	17	15	0	3
111 Jan-Mar	80	17	41	2	4
112 Apr-June	157	55	98	2	5

Fig. 1. Jaguar caught in a photo by a camera trap. Property of GVI.

Jaguar Predation

During the period of study, a total of 205 turtle carcasses were discovered (Figs. 2 & 3). Of these, 199 were green turtles, three were leatherback turtles (1.5%) and the three remaining were hawksbill turtles (1.5%). One of the greens was deemed to have died of natural causes and so is irrelevant to this study, leaving 198 green turtles (97.1%) and 204 total carcasses.

Seventy-six (37.3%) of the carcasses were located in the vegetation vertical position. Thirty-seven (18.1%) of the carcasses were in the border vertical position. Ninety-one (44.6%) of the carcasses were in the open vertical position. One-hundred-seventy-five (85.8%) turtle carcasses were found lying on their front, while the rest (14.2%) were found lying on their backs. There were seven categories for days since kill (DSK) for the turtles: 21 (10.3%) were <24hrs; 33 (16.2%) were 1-2 days; 42 (20.6%) were 2-4 days; 45 (22.1%) were 4-7 days; 32 (15.7%) were 7-14 days; 22 (10.8%) were 14-21 days; and 9 (4.4%) were 21+ days. Parts eaten and point of attack was extremely hard to determine most of the time. Only 23 instances were recorded, most of these being the neck and occasionally head and flippers along with neck as far as parts that were eaten.

Vertical position was compared to nearest northern mile marker (NNMM). The highest number of carcasses located in the vegetation vertical zone occurred at mile marker 13 (nine carcasses) (Fig. 4). The highest number of carcasses located in the border vertical zone occurred at mile markers 10 and 13.5 (four carcasses). The highest number of carcasses found in the open vertical position occurred at mile markers 12.5 and 15 (seven carcasses).

The number of carcasses were also compared to the nearest northern mile maker (NNMM). As seen in Fig. 5, most carcasses were located at mile marker 13.

Fig.2. Close-up and landscape photos of turtle carcasses. (A) is a close-up of a dead turtle showing the identification plate. (B) and (C) were landscapes of turtle carcasses indicating the surroundings where they were killed. Property of GVI.

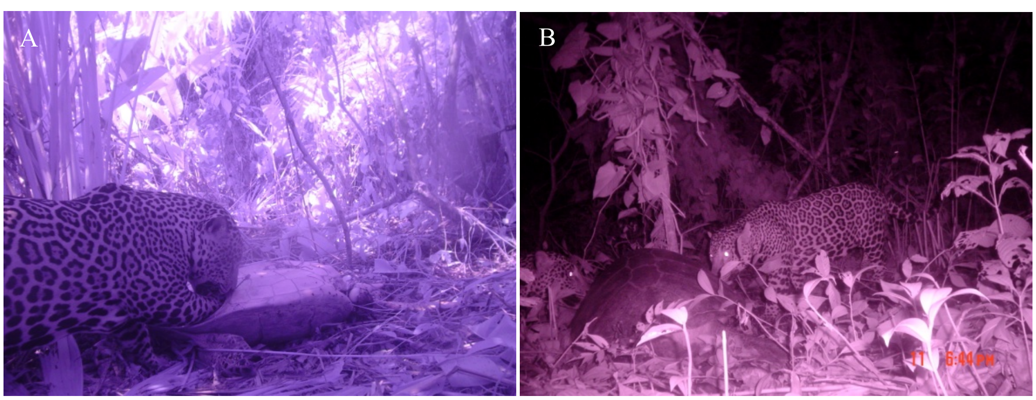

Fig. 3. Jaguars eating turtles. (A) is a photo taken by a camera trap placed on site of a turtle carcass. The jaguar returned the carcass to eat more. It is scooping out the insides of the turtle using its paw. (B) shows two jaguars sharing a kill, a rare occurrence. Property of GVI.

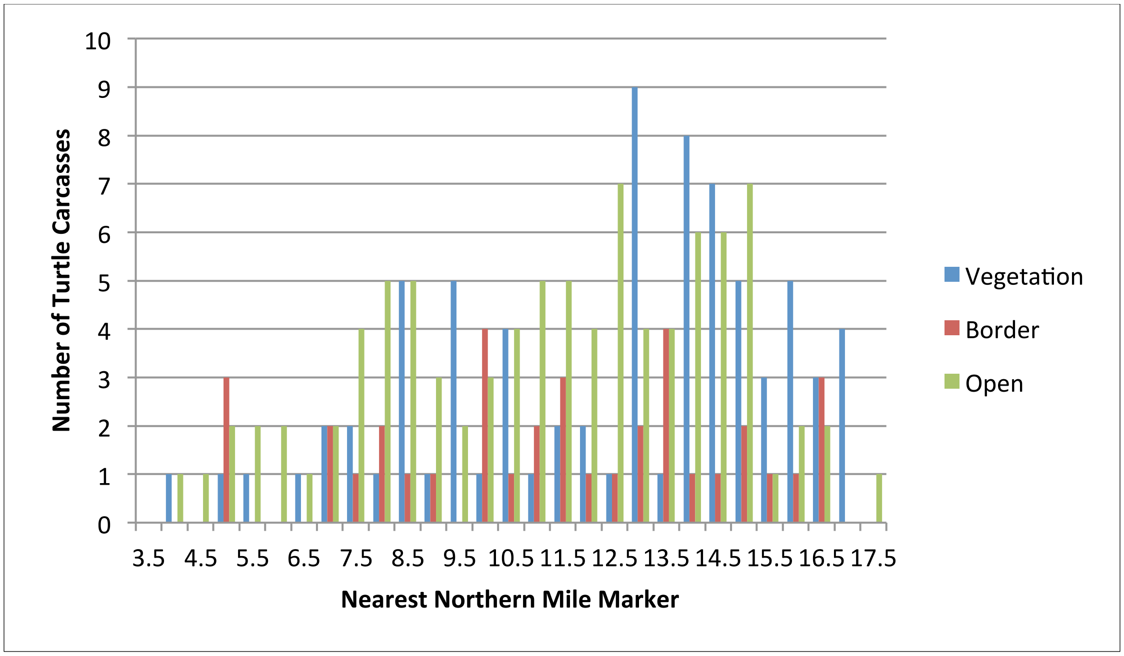

Fig. 4. Vertical position of turtle carcasses compared to nearest northern mile marker (NNMM). At each mile marker, each turtle carcass was recorded in a specific vertical position on the beach. These vertical positions have an impact on rate of decay and where the jaguar is killing/eating prey.

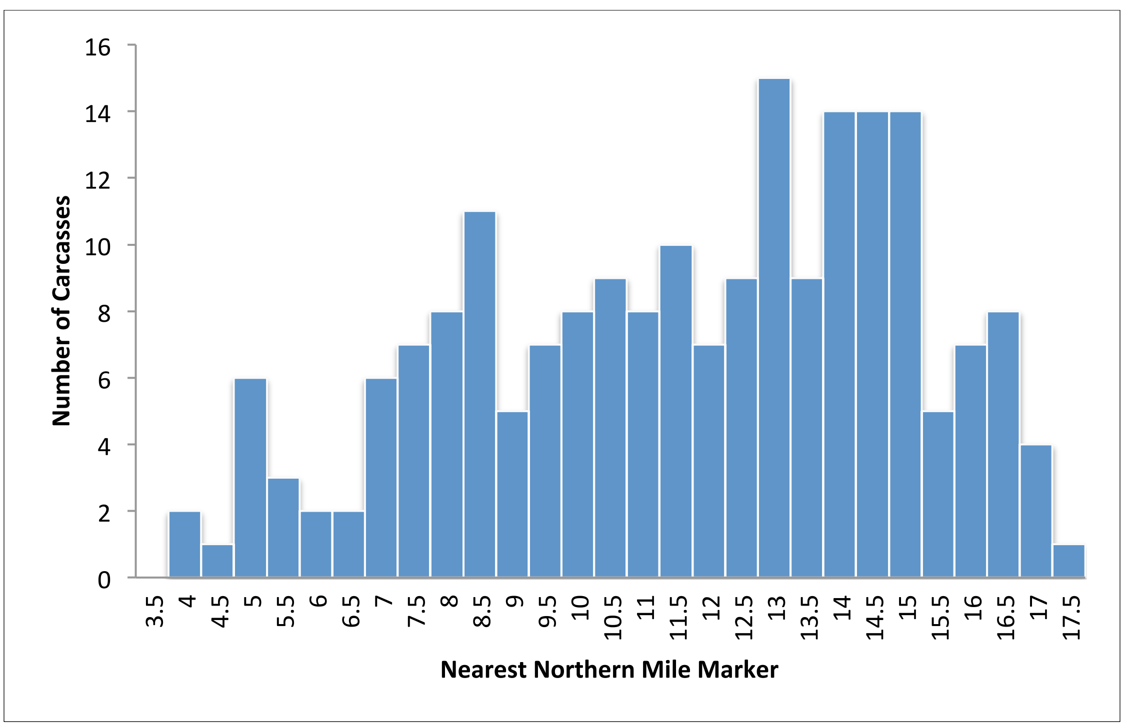

Fig. 5. Turtle carcasses per nearest northern mile marker (NNMM). This graph shows the amount of turtle carcasses (green, leatherback, and hawksbill) found in each mile marker section.

Jaguar Activity

Jaguar tracks were recorded on 34 surveys. A total of 633 instances of tracks were documented. These instances were then compared to the nearest northern mile marker (NNMM). Tracks were most often seen at mile marker 13 (Fig. 6).

Not only was presence of jaguar tracks recorded, but also their entry and exit points on and off the beach. A total of 290 entry and exit points were recorded on 52 different surveys. There were 153 (52.8%) entry points and 137 (47.2%) exit points. The jaguar entry/exit points were compared to the nearest northern mile marker (NNMM). Most entrances occurred in mile marker 13 (13 entrances) while most exits occurred at mile markers 11 (11 exits) (Fig. 7). The frequency of these entry/exit points was then compared to the number of carcasses found in the same mile marker. The r value shows that there is a significant positive correlation between the number of entry/exit points in an area and the number of turtle carcasses found ($r = 0.724$; $p < 0.05$).

These track frequencies were also examined by the date. The survey date where there was the highest frequency of jaguar tracks was on 2/10/11 as can be seen in Fig. 8.

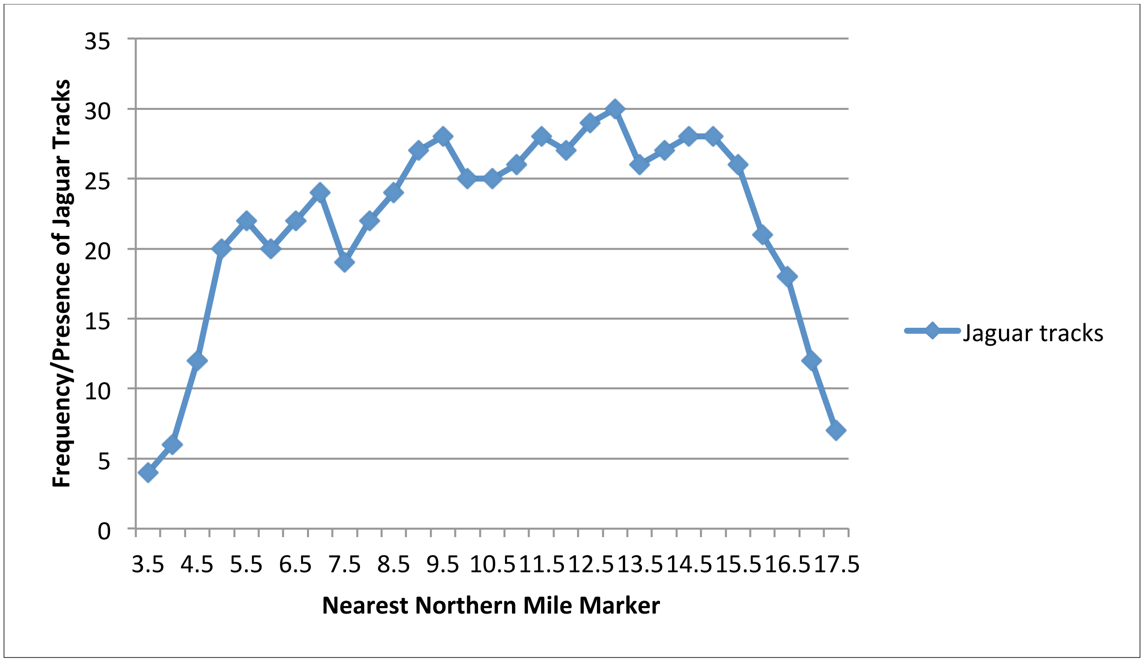

Fig. 6. Presence of jaguar tracks per nearest northern mile marker (NNMM). This graph shows the number of instances jaguar tracks were indicated as present at each mile marker.

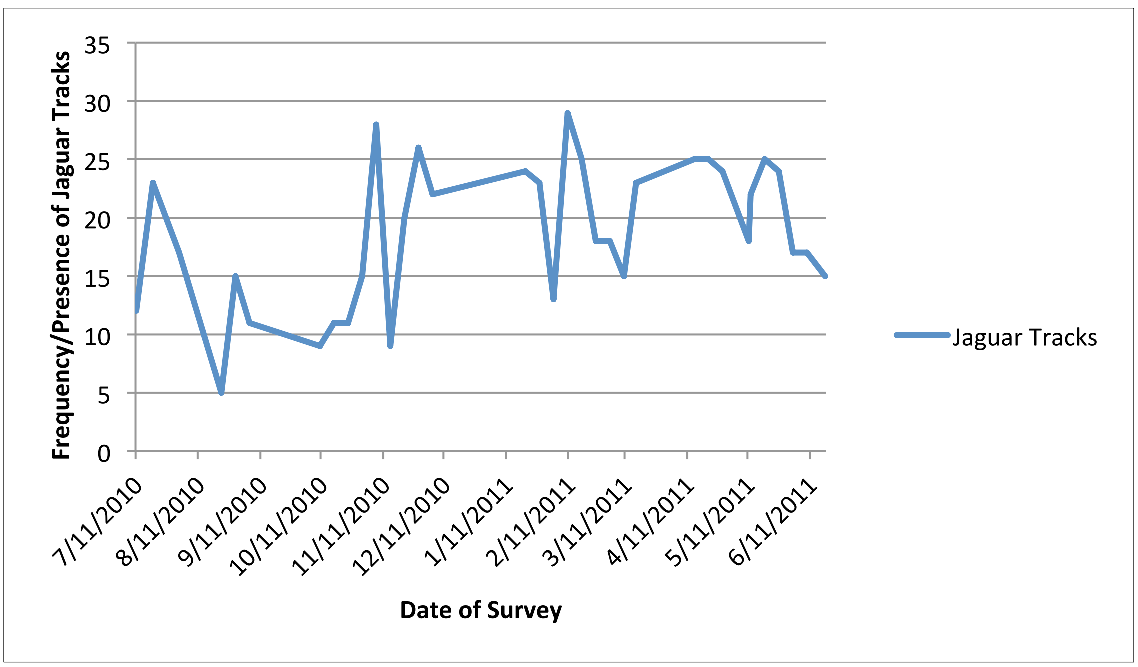

Fig. 7. Presence of jaguar tracks per time of year. This graph indicates the number of mile markers jaguar tracks were indicated as present on each survey throughout the year. The maximum number of mile markers tracks could be present is twenty-nine.

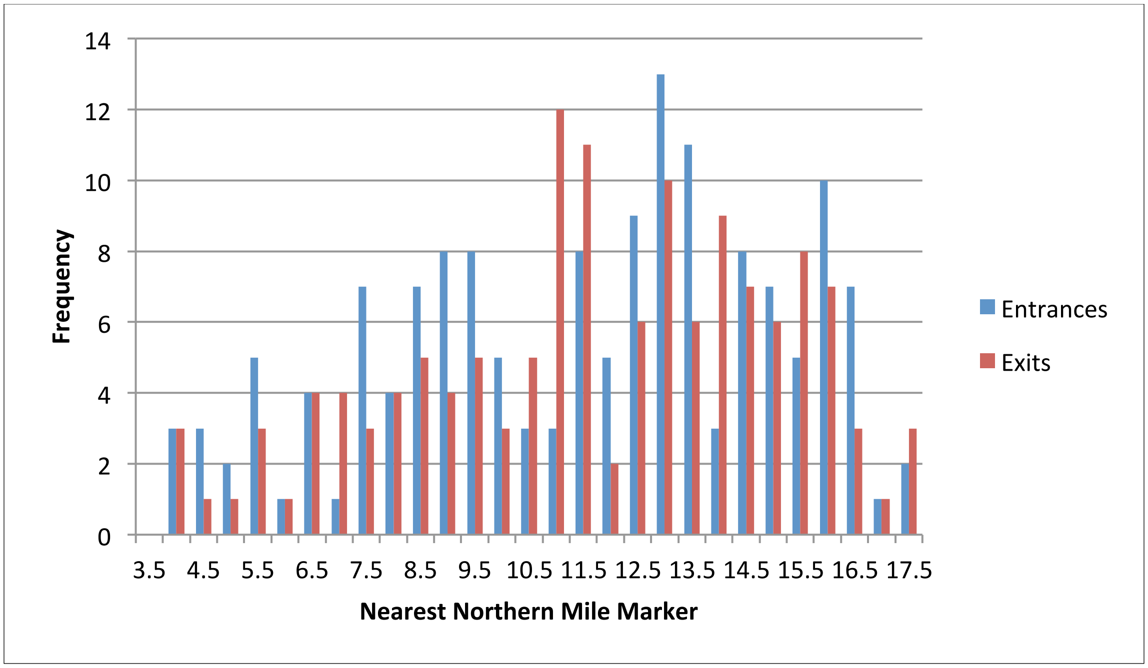

Fig. 8. Frequency of Entry/Exit points per nearest northern mile marker (NNMM). Entry points, where the jaguar entered onto the beach from the vegetation, and exit points, where the Jaguar exited the beach into the vegetation, were recorded when seen. This points were compared to the nearest northern mile marker to show which mile marker sections jaguars entered/exited at the most.

Green Tracks

Frequency of green turtle tracks was recorded on 35 surveys. A total of 38,933 tracks were recorded overall. This number was broken into half-moons and full tracks. A total of 1,126 (2.9%) half-moon tracks were documented. A total of 37,807 (97.1%) full tracks were documented. These frequencies were then compared to nearest northern mile marker (NNMM). Most half-moon tracks were seen at mile marker 15 while most full tracks were seen at mile marker 9.5 (Fig. 9).

These frequencies were also examined by the date. Most half-moon and full tracks occurred in August, particularly on August 29, 2010 (Fig. 10). On this date, 10,686 tracks were recorded.

The correlation between green half-moon and full tracks as compared to mile marker was then compared to the Jaguar Track Data. The resulting r value shows that there is a significant positive correlation between the number of green turtle half-moon tracks in an area where there was also a high frequency of jaguar tracks and exit/entry points ($r = 0.921$; $p < 0.05$). The resulting r value also shows that there is a significant negative correlation between the number of green turtle full tracks in an area and the frequency of jaguar tracks and exit/entry points ($r = -0.897$; $p < 0.05$).

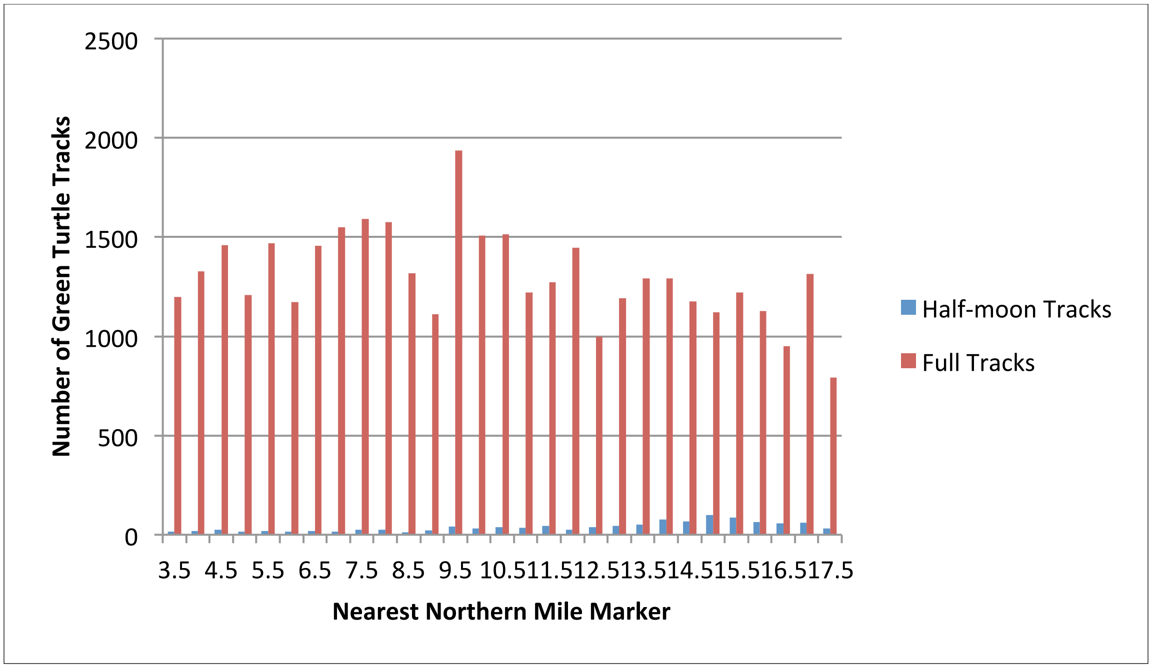

Fig. 9. Number of green turtle tracks per nearest northern mile marker (NNMM). Every half mile, the number of both green half-moon and full tracks were recorded. This shows the areas of highest turtle activity.

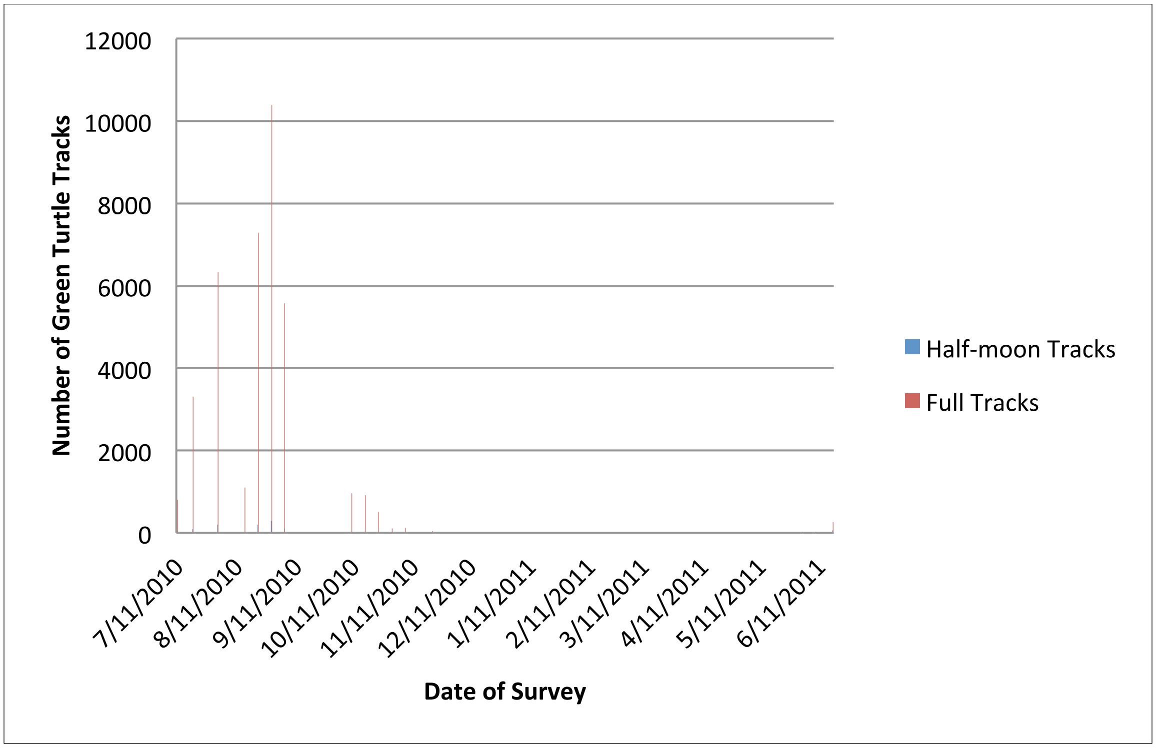

Fig. 10. Number of green turtle tracks per time of year. This graph indicates how many green half-moon and full tracks were recorded each survey over the one year time period.

Leatherback Tracks

Frequency of leatherback tracks was recorded on 12 surveys. The total number of tracks collected was 120. This number was divided into half-moons and full tracks. A total of 22 (18.3%) half-moon tracks were documented. A total of 98 (81.7%) full tracks were documented. These frequencies were then compared to nearest northern mile marker (NNMM). The highest frequency of half-moon tracks was seen at mile marker 9 while the highest frequency of full tracks was seen at mile marker 17 (Fig. 11).

These frequencies were also examined by date. The highest frequency of both half-moon and full tracks occurred during May but the most recorded at one time was on April 14, 2011 (Fig. 12). On this date, 46 tracks were observed.

The correlation between leatherback half-moon and full tracks as compared to mile marker was then compared to the jaguar track data. The resulting r value shows that there is a significant positive correlation between the number of leatherback half-moon tracks in an area where there was also a high frequency of jaguar tracks and exit/entry points ($r = 0.765$; $p < 0.05$). The resulting r value also shows that there is a significant negative correlation between the number of leatherback full tracks in an area and the frequency of jaguar tracks and exit/entry points ($r = -0.819$; $p < 0.05$).

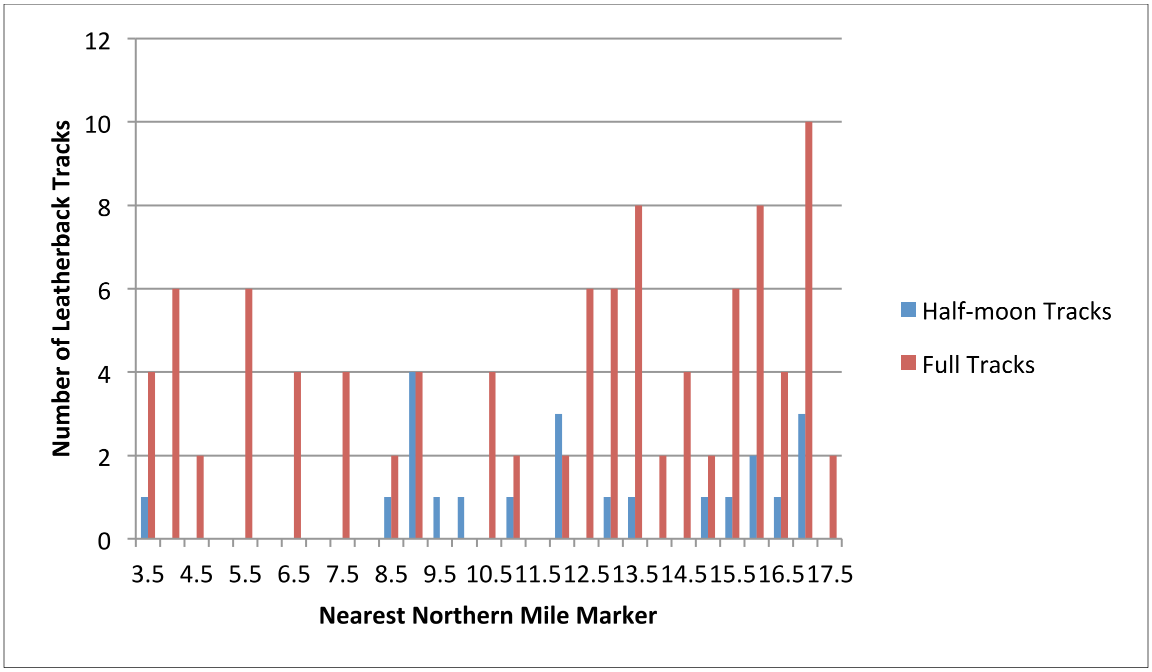

Fig. 11. Number of leatherback turtle tracks per nearest northern mile marker (NNMM). Every half mile, the number of both leatherback half-moon and full tracks were recorded. This shows the areas of highest turtle activity.

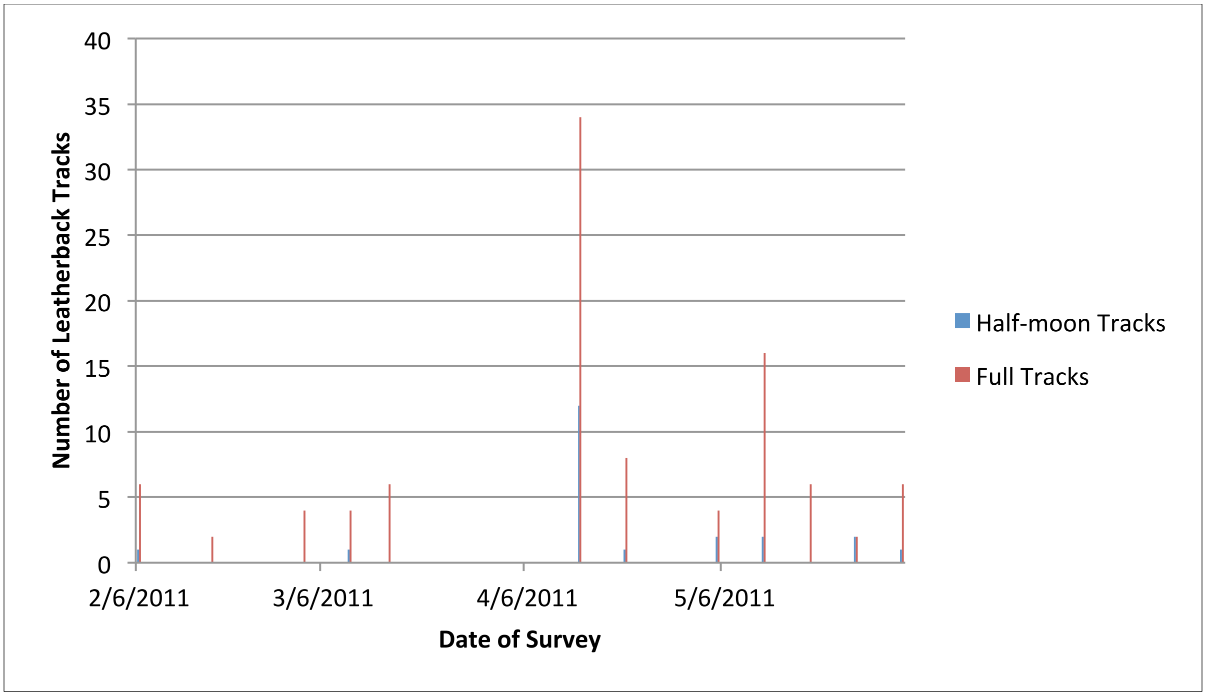

Fig. 12. Number of leatherback turtle tracks per time of year. This graph indicates how many leatherback half-moon and full tracks were recorded each survey over the four month time period.

Conclusions

By setting up 89 different cameras and taking photos/videos over a period of 251 days total, 154 pictures of jaguars were taken. Using these photographs, individuals were identified from their unique rosette markings (Silver et al., 2004). All together, a total of 5 adult jaguars were identified.

Four of these jaguars had been captured on camera more than once and over a period of time. This seems to indicate that there were perhaps 4 resident jaguars in the area. These 4 may have permanent territories that include parts of the park where the cameras have been located.

The fifth jaguar was not recaptured on camera. This could mean that it is a non-resident, and therefore just passing through. Another possibility is that its territory may only include a small section of the park where it does not frequent often or where the cameras were rarely placed.

It should be noted that there were photos showing two jaguars together (Fig. 3B). This is a rare occurrence, since jaguars were known to be solitary cats (Eisenberg, 1989). The exception to this rule is when a mother has cubs or during mating season (Eisenberg, 1989). However, from the photos taken, it appears that these jaguars were both males. This is even more strange since male jaguars were known to have large, fairly non-overlapping (Kitchener, 1991). It is speculated that this pair were young adults from the same litter. This cooperative behavior may be due to this factor and the males had yet to separate.

Although 5 individuals have been identified in the park so far, this is only a minimum number. There could be more jaguars passing through or more residents. They may not have been caught on camera because they do not use the trails where the cameras were placed or because their territories were located in a part of the park where cameras were not located. The North trail is parallel to the beach and runs quite close to it. If a jaguar did not regularly go on the beach or was located in the back (western) part of the park, it is unlikely to have been captured on camera. In order to get a better estimation of the actual population of jaguars residing in the park, more cameras should be placed at an even greater variety of locations.

Over the period of study, a total of 204 turtle carcasses were found (discounting the one that died of natural circumstances). One-hundred-ninety-eight (97.1%) of these were green turtles, 3 (1.5%) were leatherbacks, and 3 (1.5%) were hawksbills. This is not surprising as there were infinitely more greens nesting on the beach than either leatherbacks or hawksbills. Also, leatherbacks were extremely large and were unable to be drug into the vegetation by the jaguars, so this may have deterred predation.

This total number of carcasses was compared to the nearest northern mile marker. The mile marker with the highest frequency of carcasses was mile 13. This is also the mile marker that has the highest frequency of jaguar tracks and entry/exit points. Jaguars may have been present here most often due to the large amount of turtles that were coming onto the beach, and therefore preyed on a large number of them. However, there may not have been any more turtles nesting here than anywhere else, but due to the fact that jaguars were entering, exiting and walking the beach at this point, more turtles were preyed upon.

The mile markers with the lowest frequency of turtle carcasses were those nearest the most northern and southern parts of the beach. The mile marker closest to town (3.5) had no turtle carcasses recorded there at all. This is probably due to the human traffic that has been noted for jaguar tracks and entry/exit points. Either there were fewer turtles coming onto the beach at these places due to human activity, and therefore fewer were being preyed upon, or jaguars were less likely to prey upon the turtles due to their avoidance of human activity.

As far as the vertical position of the beach where the turtles were found, 76 (37.3%) were located in the vegetation, 37 (18.1%) were located in the border, and 91 (44.6%) were found in the open. I found this surprising because jaguars were thought to often carry their prey back into the vegetation, according to the staff on site. Many may have been left in the open due to some disturbance. Many carcasses were found still bleeding, so we may have disturbed the jaguar before it had a chance to drag it. Other humans sometimes walk the beach and this could also have disturbed the jaguars.

Leatherbacks were all found in the open due to the fact that they were too heavy for the jaguar to drag. This may also show that the majority of turtles were killed either headed up the beach to nest, or back to the water. Only the leatherback nests in the middle of the beach while the green and hawksbill nest in the vegetation or along the vegetation line (Bonin, Devaux, & Dupre´, 2006). Had they been killed while in the vegetation or along the line, they would not have been dragged back into the open, and therefore remained in the vegetation or on the border.

Vertical position was also compared to the nearest northern mile marker (NNMM). Of the carcasses found in the vegetation, most of these occurred in mile 13. Most of the carcasses found at the border occurred at miles 10 and 13.5. Finally, the highest number of turtles found in the open occurred at miles 12.5 and 15. This information might indicate what type of habitat was at that location. For example, miles 12.5 and 15 might have had thick vegetation that would not allow a turtle to be dragged through. The opposite may be said for mile 13. Mile 13 is also where the highest number of jaguar track presence and entry points were. Perhaps this location is a frequented path where the jaguar feels comfortable dragging the turtles into the vegetation.

Of the 204 carcasses found, 175 (85.8%) of these were on their fronts and the other 29 (14.2%) were found on their backs. This may be because the jaguars left them in the position in which they were killed. Jaguars often kill with a bite to the head or neck which would easily be accessed while the turtle was on its front (Navarro-Serment, López-González, & Gallo-Reynoso, 2005). In order to scoop out the insides of the turtle, the jaguar would sometimes flip the turtle onto its back, so as to more easily insert their paw. Again, due to size and weight, the leatherbacks were all found on their fronts.

Interestingly, all 3 hawksbills were found lying on their backs. This may show that jaguars eat hawksbill turtles differently than green turtles, which are their normal prey. Louise Emmons, during his study of jaguar predation on Chelonians, did notice that the cats had a different way of accessing the shells of different species of turtles (1989).

Carcasses were found in all increments of days since killed (DSK). Twenty-one (10.3%) were <24hrs; 33 (16.2%) were 1-2 days; 42 (20.6%) were 2-4 days; 45 (22.1%) were 4-7 days; 32 (15.7%) were 7-14 days; 22 (10.8%) were 14-21 days; and 9 (4.4%) were 21+ days. Days since killed was often hard to determine since characteristics were subjective to interpretation. Each turtle was determined to have been for a certain number of days due to whether it had or lacked certain physical characteristics. Usually the carcasses did not fit all the descriptions of a specific time period and best guesses were taken. Also, weather and location can have a big effect on decomposition. If there had been extremely hot weather, if it was located in direct sunlight, or if it was lying on its back, the turtle may exhibit more decomposition than a turtle killed the same day, but under different conditions. It is likely that a carcass will be found within 7 days since a survey is taken once a week. A turtle carcass that is older than 7 days may have been dragged out of the vegetation. By determining the days since a turtle was killed, it was possible to identify when jaguars were preying upon the highest amounts of turtle. Perhaps in a future study, days since killed (DSK) could be compared to jaguar activity and also to abiotic factors, such as weather.

Parts eaten and point of attack were extremely hard to determine. Only on 23 out of the 204 carcasses was it recorded what parts were eaten and the likely point of attack. The majority of the time, the neck was the point of attack and the only, or one of, the parts eaten. Other times, the head and flippers were also eaten. As referenced in vertical position, jaguars were recorded as killing prey by a strong bite to the head or neck (Navarro-Serment, López-González, & Gallo-Reynoso, 2005). Kitchener (1991) adds that jaguars were recorded as initially feeding on the neck, chest, and forequarters. Our data reflects this and helps demonstrate how jaguars kill their prey as compared to other big cats.

Jaguar track presence was recorded 633 times over a total of 34 surveys. When compared to the nearest mile marker, tracks were most often seen at mile marker 13. This stretch is located on near the southern end of the second third of the surveyed beach, closer to the Jalova River mouth. Most of the tracks did occur in the second third of beach, favoring neither the third located closest to town or closest to the river. There is a decline in track presence the closer the mile marker is to town or the river mouth. Both of these areas were more heavily trafficked by humans. Though the Jalova River mouth is not nearly as populated as town, boats do use it to access the sea and our base is located close to it.

Jaguar track presence was also examined by date. The survey date with the highest frequency of jaguar track presence was in February, 2011. There was an overall increase in the presence of jaguar tracks. During the fall months, there were fewer than in the winter, spring, and early summer. What is surprising is the low presence of tracks during the peak of green nesting season. There were high frequencies of jaguar presence during the leatherback nesting season, but also during the winter months when there were no turtles nesting.

Some observations made were that the jaguar tracks were often parallel to the sea.

They would walk long stretches of beach before heading back into the vegetation. This seems to show that they were actively looking for prey, specifically the turtles. Also, just as with the jaguar photos, two sets of prints were often seen together. They were relatively the same size, so it was unlikely to be a mother and cub. It is possible that these tracks were made on different days. It should also be noted that it was often difficult to determine if the tracks were fresh. Depending on the sand conditions, the tracks varied in appearance. For example, in damp sand, fresh tracks were distinct and had sharp, defined edges. However, in dry sand, tracks were less distinct and sand had often fallen back into the track. Because of this, it was hard to establish how fresh these tracks were.

Also, specific entry and exit points of the jaguars on and off the beach were examined. A total of 290 entry/exit points were recorded on 52 surveys. One-hundred-fifty-three (52.8%) of these were entry points and 137 (47.2%) were exit points. Though the numbers were not drastically uneven, there were more entry than exit points. This could simply be due to sampling error. Both entry and exit points were hard to identify due to sand conditions and vegetation. Where the vegetation and beach meet, the sand is very dry and many vines were creeping out onto the beach. Because of this, it was hard to identify any tracks, much less fresh ones. Also, the jaguars would sometimes walk along the vegetation and seem to go in, but not completely. They would actually be walking on the vegetation line where tracks were hard to observe. This could lead to an increase in entry points. Also, jaguars may use the same points along the beach as both entry and exit points, perhaps due to the thin vegetation or location of a particular path. Due to this, it could be that it was difficult to ascertain which tracks were the freshest and if they were ingoing or outgoing, since both were located there. Finally, if a jaguar exited the beach with a turtle, their tracks may be obscured since the turtle would be dragged. This could certainly give an appearance of more entries than exits.

As with the jaguar tracks, entry/exit points were compared to nearest northern mile marker (NNMM). The results of this show that the most entry points were located at mile 13 and most exit points were located at mile 11. The frequency of entry points at mile 13 corresponds with the highest frequency of jaguar track presence at mile 13. The half of the beach closest to the river seems to have more entries/exits than the half of the beach closest to town. This is likely the result of human traffic closer to town. There were also higher numbers of exits on the southern half of the beach, while there were more entrances than exits on the northern half of the beach. This may show that the jaguars would enter onto the northern half of the beach more often than they would exit. Perhaps this shows an overall southward movement.

The relationship between the frequency of entry/exit points and the number of turtle carcasses found in the same mile marker section were statistically analyzed. The r value shows that there is a significant correlation between the number of entry/exit points in an area and the number of turtle carcasses found ($r = 0.724$; $p < 0.05$). The more entry/exit points were in an area, the more turtle carcasses were found there. This may point to the fact that a jaguar would enter onto the beach if it sensed there were turtles there and then quickly dispatched of one. This sensing could be olfactory, auditory or visual. This result might also show that a jaguar would enter onto the beach and kill the first turtle it encountered, which happened to be in the same mile marker section. Regarding exits, a jaguar may prey on a turtle and then exit the beach, leaving the carcass due to some disturbance or its inability to move it. Jaguars often drag their prey into the vegetation as well, so these exits may be from where turtles were dragged in.

The frequency of green turtle tracks was recorded on 35 surveys, resulting in the overall number of 38,933 tracks. Of this number, 1,126 (2.9%) were half-moons while the other 37,807 (97.1%) were full tracks. Half-moons were normally where the turtle comes onto the beach, but for some reason turns around without successfully nesting. This did not happen very often as compared to actual nesting, which is what a full track normally indicates. Therefore, turtles came fully onto the beach and instead of arching, turned directly around (usually having made a nest) about 18,903 times. Although this number may seem staggering, each turtle can lay up to 6 nests and Tortuguero Beach is listed as one of the green turtles' preferred nesting sites (Bonin, Devaux, & Dupre´, 2006).

These frequencies were compared to the nearest northern mile marker (NNMM). Most half-moon tracks occurred at mile 15. In general, most of the half-moon tracks occurred on the southern half of the beach, closest to the river mouth. The mile marker with the highest frequency of full tracks was mile 9.5. Although the amount of full tracks seems relatively even along the entire beach, there is a slight overall increase of tracks on the northern half of the beach, located closest to town.

This relationship between the frequency of tracks and mile marker was then compared to the presence of jaguar tracks/entry and exit points. The resulting r value shows that there is a significant correlation between the number of green turtle half-moon tracks in an area where there was also a high frequency of jaguar tracks and exit/entry points ($r = 0.921$; $p < 0.05$). Therefore, where there was more jaguar activity, there were also more half-moon tracks. This has several implications. One is that the turtles may have been spooked by the jaguar activity and headed back to the water instead of nesting. Turtles have good vision only in the water, so it seems unlikely that they would have been alarmed visually (Sea turtles, 2011). However, sea turtles do have good hearing and an extremely keen sense of smell, so they may have heard the jaguars or smelled them (Sea turtles, 2011). Due to past research done on chemosensory and olfaction in sea turtles, it seems that turtles are able to pick up chemical cues or odor molecules from their environment (Grassman, & Owens, 1987; Hochscheid, Maffucci, Bentivegna, & Wilson, 2005) Hochschied (2005) discusses how sea turtles use their vomeronasal epithelial lining in their buchal (mouth) cavity to perceive dissolved substances in the water. Perhaps the turtles can also do this out of the water, when they are attempting to nest. Not only might they have smelled the jaguar, but since this was also the highest area of predation, they may have smelled the dead turtles on the beach.

Such a theory could be tested by spraying different plots of a shoreline with the scent of jaguars or dead turtles. If there was no actual presence of jaguars and the turtles were significantly avoiding the scented areas, then it could be concluded that they must be using some sort of chemosensory function. However, due to the endangered status of sea turtles, such a test would most likely not be conducted on an actual nesting beach. Perhaps juveniles could be used and an artificial nesting beach could be prepared.

The other resulting r value also shows that there is a significant negative correlation between the number of green turtle full tracks in an area and the frequency of jaguar tracks and exit/entry points ($r = -0.897$; $p < 0.05$). This means that when there is more jaguar activity, there were less full tracks in that area or vice versa, which is the opposite of what the result was for half-moon tracks. However, though these correlations were opposite, perhaps they were due to similar reasons. Just as the turtles may somehow sense when there is jaguar activity or presence of other turtle carcasses as mentioned previously, so too might they be able to sense the lack of these things. If they do not smell, hear, or (possibly) see a jaguar, this may lead them to conclude that the area is safe to nest in. Also, if they do not smell the presence of dead turtles, this too may lead them to conclude that the area is relatively safe. These safe nesting areas may change over time, especially if the jaguars learn that there were current places where many turtles were nesting. If the jaguars then start frequenting these sites, predation may rise and the turtles might stop using these sites and move on to a different area of the beach where the jaguar activity is less.

Finally, the frequencies of tracks were also compared to the date. Most of the tracks, both half-moon and full, occurred in August, 2010. This result is not surprising, since this is the height of green turtle nesting season.

Abiotic factors such as weather and sand conditions were examined as a potential reason for presence of turtle activity. However, at this time, there seems to be no correlation between the two. Perhaps in the future, more detailed information about these factors, such as the vertical height of the beach, could be recorded.

Frequency of leatherback tracks was recorded on 12 surveys, resulting in 120 tracks. Of this number 22 (18.3%) were half-moons and 98 (81.7%) were full tracks. Just as with the green tracks, a half-moon is when the turtle makes an arch on the beach turning around without nesting, and a full track usually indicates nesting and is counted as 2. Therefore, theoretically, about 49 turtles came fully onto the beach and nested. This number is much smaller than the green turtles, but is justified due to the fact that

Tortuguero is not labeled as a preferred nesting site for the leatherback and they were often seen there.

As with the green tracks, the frequency of leatherback tracks was compared to nearest northern mile marker (NNMM). The mile with the highest number of half-moons was 9 and most half-moons occurred on the southern half of the beach closest to the river mouth. Very few occurred on the northern half of the beach, with mile markers 4-8 having none at all. The mile marker with the highest number of full tracks was 17. The leatherback full tracks were fairly even along the beach, but the three mile markers with the highest frequencies were all on the southern half. This is opposite of what the green full tracks showed. This may show that the leatherbacks were more wary of the human traffic closer to town than the greens were.

The relationship between the leatherback half-moon and full tracks and mile markers was also correlated to jaguar track data. The resulting r value shows that there is a significant correlation between the number of leatherback half-moon tracks in an area where there was also a high frequency of jaguar tracks and exit/entry points ($r = 0.765$; $p < 0.05$). This is the same result as with the green turtles. It shows that where there was more jaguar activity (tracks/entry and exit points), there were also more half-moon tracks. The suggestions as to why this may occur were the same as those made for the green turtles.

The other resulting r value also shows that there is a significant negative correlation between the number of leatherback full tracks in an area and the frequency of jaguar tracks and exit/entry points ($r = -0.819$; $p < 0.05$). This means that when there is more jaguar activity, there were less full tracks in that area or vice versa. The correlation between the half-moon tracks and jaguar activity was just the opposite of this. Conclusions as to why this may be happening were the same as those discussed for the green turtles.

These frequencies were also examined by date. The highest frequency of both half-moon and full tracks occurred during May. However, the specific date with the most tracks recorded was in April, 2011. This difference could be accounted for by noting that more surveys were taken in May than in April. Even with this difference, only two out of four surveys in April were any tracks recorded. The late spring is the nesting season of the leatherback and our data corroborates this.

As with the green turtles, biotic factors such as weather and sand conditions were examined as a potential reason for presence of turtle activity. However, at this time, there seems to be no correlation between the two.

After examining all of the data collected during this study, the relationship between jaguars and their prey of sea turtles seems to be a complex one. If, as speculated with the correlation between green/leatherback tracks and jaguar activity, that the turtles are reactive to the presence jaguars, then this has conservation implications. Turtle conservation needs to be a primary goal if Tortuguero is to remain listed as an important nesting site for both green and leatherback turtles. If the turtles are negatively impacted by the presence of predators (jaguars), then a way to either lower the presence, or impact, of jaguars should be found.

This could perhaps be accomplished by increasing the availability of a preferred food source, so the jaguars would not need to prey upon sea turtles. A result of the optimal foraging theory is that when preferred prey density drops below a certain point, the predator will switch to an alternative food source (van Baalen, Křivan, van Rijn, & Sabelis, 2001). This result may account for the increased predation of sea turtles by the jaguar in Tortuguero.

One way to increase the density of preferred prey species of the jaguar is to more strictly enforce poaching. As stated earlier, the jaguar's main prey is mammals, so by decreasing the poaching rate of mammals in the park, the jaguars will have more to eat (de Oliveira, 2002). The jaguars may eat more mammal species if there are higher densities of them, since the amount of each species that composes a jaguars diet is mirrored by the density of each prey species in an area (Kitchener, 1991).

Increasing the jaguar's available food source might also be accomplished by decreasing deforestation. Right now there are possibly 4-5 resident jaguars at Tortuguero. There may not be enough mammalian prey in the area to sustain this number, and so the jaguars are forced to eat larger amounts of turtles. By decreasing deforestation, these jaguars may increase their territories so as to encompass more prey. This would reduce the stress on the currently available prey populations in the park so that their numbers can multiply. These prey populations will also benefit from decreased deforestation, by having more area and resources to utilize.

In several cases, it was also speculated that human traffic may have a negative impact on both turtle and jaguar activity, and thus the interaction between them. In order to facilitate both sea turtle nesting and jaguar presence, human traffic should be kept at a minimum along the beach. Although increased patrolling on a beach by researchers decreased the amount of poaching that occurred, increasing the survivorship of sea turtles, this may come at an expense (García, Ceballos, & Adaya, 2003). The closer to town, and the more human traffic that occurred, the less jaguar activity occurred. Although this may decrease the amount of sea turtles predated upon, the jaguar needs a stable food source. If the jaguars are predating upon the sea turtles due to stresses on food supply, this would decrease the viability of the jaguars. All of the species in this study are listed by the Convention of International Trade in Endangered Species as an Appendix I species (CITES, 2011). Both the turtles and the jaguars are declining in numbers and efforts must be taken to help the survival of both creatures. With this in mind, it is important that the remaining turtles and jaguars be impacted as little as possible so they can go about their normal behaviors and interactions without the fear or interference of humans.

This study addresses some aspects of the predator-prey interactions between these two species. The better scientists understand this relationship, the better they will be able to make decisions about conserving these declining species. Only with further research can a better understanding be achieved.

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References

Autar, L. (1994). Sea turtles attacked and killed by jaguars in Suriname. *Marine Turtle Newsletter, 67*, 11-12. Retrieved from: http://www.seaturtle.org/mtn/archives/mtn67/mtn67p11.shtml

Bonin, F., Devaux, B., & Dupre´, A. (2006). *Turtles of the world* (P.C.H. Pritchard, Trans.). Baltimore, MD: The Johns Hopkins University Press.

Carrillo, E., Fuller, T.K., & Saenz, J. (2009). Jaguar (*Panthera onca*) hunting activity: Effects of prey distribution and availability. *Journal of Tropical Ecology, 25,* 563-567. doi: 10.1017/S0266467409990137

CITES. (n.d.). “What is CITES?” Retrieved from: http://www.cites.org/. Dec. 5, 2011.

Costa Rica national parks. (2009). “Tortuguero National Park.” Retrieved from: http://www.costarica-nationalparks.com/tortugueronationalpark.html. Dec. 5, 2011

Da Silveira, R., Ramalho, E.E., Thorbjarnarson, J.B., & Magnusson, W.E. (2010). Depredation by jaguars on caimans and importance of reptiles in the diet of jaguar. *Journal of Herpetology, 44*(3), 418-424. Retrieved from: http://journals.ohiolink.edu/ejc/pdf.cgi/Da_Silveira_Ronis.pdf?issn=00221511&issue=v44i0003&article=418_dbjocaritdoj

de Oliveira, T.G. (2002). Comparative feeding ecology of jaguar and puma in the neotropics. *Universidad Nacional Autónoma de México/Wildlife Conservation Society*. Retrieved from: http://www.jaguarnetwork.org/pdf/175.pdf

Eisenberg, J.F. (1989). *Mammals of the neotropics: The northern neotropics* (Vol. 1). Chicago, IL: The University of Chicago Press.

Emmons, L.H. (1989). Jaguar predation on chelonians. *Journal of Herpetology, 23*(3), 311-314. Retrieved from: http://jstor.org/stable/1564460

García, A., Ceballos, G., & Adaya, R. (2003). Intensive beach management as an improved sea turtle conservation strategy in Mexico. *Biological Conservation*, *111*(2), 253-261.

Grassman, M., & Owens, D. (1987). Chemosensory imprinting in juvenile green sea turtles, (*Chelonia mydas*). *Animal Behavior*, *35*(3), 929-931. doi:10.1016/S0003-3472(87)80133-1

Harrison, E., Troëng, S., & Fletcher M. (2005, January). *Jaguar predation of green turtles (Chelonia mydas) at Tortuguero, Costa Rica: Current trends and conservation implications.* Paper presented at the Twenty-fifth Annual Symposium on Sea Turtle Biology and Conservation, Savannah, GA. Retrieved from: http://www.nmfs.noaa.gov/pr/pdfs/species/turtlesymposium2005.pdf

Hochscheid, S., Maffucci, F., Bentivegna, F., & Wilson, R. P. (2005). Gulps, wheezes, and sniffs: how measurement of beak movement in sea turtles can elucidate their behavior and ecology. *Journal of Experimental Marine Biology and Ecology*, *316*(1), 45-53. doi:10.1016/j.jembe.2004.10.004

Kitchener, A. (1991). *The natural history of the wild cats.* Ithaca, NY: Comstock Publishing Associates.

McBride, R., Giordano, A., & Ballard, W.B. (2010). Note on the winter diet of jaguars *Panthera onca* in the Paraguyan Transitional Chaco. *Bellbird, 4*, Par. 1-12. Retrieved from: http://www.faunaparaguay.com/McBride.pdf

Navarro-Serment, C.J., López-González, C.A., & Gallo-Reynoso, J-P. (2005).

Occurrence of jaguar (*Pantera onca*) in Sinaloa, Mexico. *The Southwestern Naturalist*, 50(1), 102-106. Retrieved from: http://www.bioone.org/doi/pdf/10.1894/0038-4909%282005%29050%3C0102%3AOOJPOI%3E2.0.CO%3B2

Sea turtles. (2011). "How sharp are a sea turtle's senses?" Retrieved from: http://animals.howstuffworks.com/reptiles/turtle-info7.htm. Dec. 5, 2011.

Setchi, R., Jordanov, I., Howlett, R.J., & Jain, L.C. (Eds.). (2010). *Knowledge-based and intelligent information and engineering systems: 14th International Conference, KES 2010, Cardiff, UK, September 8-10, 2010, Proceedings, Part 1*. [Google Books]. Retrieved from: http://books.google.com/books?id=vrD8SVG9nMgC&pg=PA413&dq=pearson+correlation+coecoeffici&hl=en&ei=N0vVTpaCCcGqsALui7yGDw&sa=X&oi=book_result&ct=result&resnum=1&ved=0CDAQ6AEwAA#v=onepage&q=pearson%20correlation%20coefficient&f=false

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gomez, H., & Ayala, G. (2004). Camera traps for jaguar abundance estimates. *Oryx, 38*(2), 148-154. doi: 10.1017/S0030605304000286

Stolzenburg, W. (2008). *Where the wild things were*. New York, NY: Bloomsbury.

Troëng, S. (2000). Predation of green (Chelonia mydas) and leatherback (Dermochelys coriacea) turtles by jaguars (Panthera onca) at Tortuguero National Park, Costa Rica. *Chelonian Conservation and Biology, 3*(4), 751-753. Retrieved from: http://www.seaturtle.org/PDF/Troeng_2000a_CheloniaConservBiol.pdf

Troëng, S., & Rankin, E. (2004). Long-term conservation efforts contribute to positive green turtle (Chelonia mydas) nesting trend at Tortuguero, Costa Rica. *Biological Conservation, 121*, 111-116. doi: 10.1016/j.biocon.2004.04.014

van Baalen, M., Křivan, V., van Rijn, P.C.J., & Sabelis, M.W. (2001). Alternative food, switching predators, and the persistence of predator-prey systems. *The American Naturalist, 157*(5), 1-13. Retrieved from: http://www.entu.cas.cz/krivan/papers/amnat01.pdf

Appendix

Determining Days Since Killed

Days Since Killed	Characteristics
<24hrs	Natural coloring Pink flesh, blue veins Edges of skin supple/soft Eyes possibly intact “Perfect” carapace Blood No odor
1-2	Vulture activity (presence, tracks, scat) Bloating Flies Remaining flesh Skin starting to discolor
2-4	Maggots Putrification – strong odor Bloating Flesh turning dark grey Small scutes may start to peel
4-7	Exposed bone yellowish in color Maggots Little flesh, skin still present Odor Larger scutes may start to peel
7-14	Bones turning white Odor gone
14-21	No remaining flesh Scutes peeling off White bones
21+	Only carapace left – no/few scutes Bones starting to break apart Body cavity dry and possibly full of sand

Note. When examining turtle carcasses, the days since it was killed had to be determined. By searching for the presence (or lack of) certain characteristics, this time period can be established.

[a]Note also that the decomposition rate of a turtle flipped upside down is faster than one right-side up.