Impacts of Jaguar Predation on Nesting Sea Turtles at Nancite Beach, Santa Rosa National Park, Costa Rica

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Abstract.—Jaguar (Panthera onca) predation on sea turtles occurs across the Americas; however, records are scattered and not frequently presented in terms of their potential effects on sea turtle populations. In this study, we documented Jaguar predation events on nesting sea turtles at Nancite Beach, Santa Rosa National Park, Costa Rica, between the 2009–2010 and 2018–2019 nesting seasons (excluding 2012–2013 and 2013–2014). We also estimated the size of the local nesting populations for each sea turtle species to assess potential impacts of Jaguar predation. We documented 160 Olive Ridley Sea Turtles (Lepidochelys olivacea) and 11 Green Turtles (Chelonia mydas) that were eaten by Jaguars during our study period, corresponding to fewer than 1% and 8–40% of the nesting populations of Olive Ridley Sea Turtles and Greens, respectively. Relative to the size of each nesting population, these results suggest that Jaguar predation does not represent a significant threat to Olive Ridley Sea Turtles. Although Jaguars do not constitute a threat to Green Turtles at a regional-scale, they could influence the persistence of the nesting population at Nancite Beach if their predation rates continue over time.

Key Words.—Chelonia mydas; Lepidochelys olivacea; Panthera onca; predator-prey interaction; wild felid

Introduction

Adult sea turtles have few natural predators. In the marine environment, predators include Killer Whales (Orcinus Orca) and at least six shark species: hammerhead (Sphyra sp.), Lemon (Nagaprin brevoortis), White (Carcharodon carcharias), Bull (Carcharhinus leucas), Oceanic White Tip (C. longimanus), and Tiger (Galeocerdo cuvier) sharks (Stancyk 1981; Witzell 1987; Fergusson et al. 2000; Pitman and Dutton 2004; Heithaus et al. 2007). Nesting sea turtles also face the risk of predation on land by American Crocodiles (Crocodylus acutus; Ortiz et al. 1997), Saltwater Crocodiles (Crocodylus porosus; Whiting and Whiting 2011), Coyotes (Canis latrans; Drake et al. 2001), and Jaguars (Panthera onca; Arroyo-Arce and Salom-Pérez 2015). Throughout the Americas, Jaguar predation has been documented for five species of sea turtles (Table 1): Green (Chelonia mydas), Olive Ridley (Lepidochelys olivacea), Hawksbill (Eretmochelys imbricata), Leatherback (Dermochelys coriacea), and Loggerhead (Caretta caretta) sea turtles.

Jaguars are considered an opportunistic predator across their geographic range (Seymour 1989; Núñez et al. 2002), adapting their hunting behavior in response to prey availability (Rabinowitz and Nottingham 1986). For example, Jaguar predation events on sea turtles occur as females return to land to lay eggs, and some authors suggest that, during the peak of the nesting season, Jaguars restrict their movement to the coastal habitat as a strategy to maximize the consumption of a highly available prey item (Carrillo et al. 2009; Arroyo-Arce and Salom-Pérez 2015; Montalvo et al. 2020). Due to the conical adaptation of their canine teeth and powerful bite force, Jaguars can kill sea turtles with a crushing bite to the skull or to the neck area (Schaller and Vasconcelos 1978; this study). Then, they use their claws to reach the internal organs from the neck area (carapace, flippers, and head are not consumed). When feeding upon small species of sea turtles (e.g., Olive Ridley Sea Turtles), Jaguars may bite through the carapace as part of the feeding process. For larger species, including Leatherbacks and occasionally in Green Turtles, Jaguars can also tear the rear flippers to facilitate access, and even bite through the carapace to feed on the eggs (Escobar et al. 2016b; Ian Thomson, pers. comm.). Because Jaguars can feed from sea turtle carcasses for several days, carcasses of all species except...
Leatherbacks may be dragged deep into the vegetation to protect the remains from other wild felids (e.g., other Jaguars and Pumas, *Puma concolor*) and scavenger species (Black Vultures, *Coragyps atratus*, and Turkey Vultures, *Cathartes aura*; Guilder et al. 2015; Fonseca et al. 2018).

On Nancite Beach, located in Santa Rosa National Park, Costa Rica, Jaguar predation on sea turtles has been documented sporadically since the 1980s (Table 1). This beach is considered an important rookery for Olive Ridley Sea Turtles in the Eastern Tropical Pacific (Cornelius and Robinson 1983), as arribadas (synchronized mass nesting events) and solitary nesting occurs throughout the year (Janzen 1988; Fonseca et al. 2009). It also hosts relatively small nesting populations of Green Turtles that nest throughout the year and Leatherbacks that nest between October and February (Cornelius 1986; Fonseca et al. 2009; Herrera et al. 2016).

Prior to the establishment of Santa Rosa National Park in 1972, the landscape was dominated by agricultural and livestock farms, where illegal hunting of wild animals occurred (Janzen 1988). Since the creation of the park, however, a series of actions were adopted to protect local wildlife and their habitats, including controlling illegal activities, forest fire management, and land acquisition (Quirós-Arias 2017). Although there is little information available regarding Jaguar population estimates for Santa Rosa National Park as a whole, data has been collected at Nancite Beach as part of a long-term camera trap monitoring project started in 2010, suggesting an increase in individuals identified (Luis Fonseca et al., unpubl. report). It is likely, therefore, that recent conservation efforts have played an important role in allowing the local Jaguar population to use the coastal habitat of Santa Rosa National Park with more frequency over the years, potentially triggering predator-prey interactions between Jaguars and sea turtles (Fonseca et al. 2017). A similar pattern was observed by Arroyo-Arce (2013) and Arroyo-Arce et al. (2014), who suggested that Jaguars have been expanding their spatial distribution to nesting beaches inside protected areas, causing the felids to increasingly select sea turtles as prey. As a result, it is crucial to monitor and assess the effects of this interaction so that conservation efforts can ensure adequate co-management of these flagship species. The goals of our study were to quantify the number of Jaguar predation events on nesting sea turtles on Nancite Beach and to compare the number of turtles predated annually by Jaguars with the size of the local nesting population for each turtle species. These data will provide a baseline for understanding the threat posed by Jaguars on these nesting populations.

**Materials and Methods**

**Study Site.**—Nancite Beach is located on the north-west Pacific coast of Costa Rica (10°48′12″N, 85°41′47″W) within the Santa Rosa National Park, Guanacaste Conservation Area (Fig. 1). The beach is
### Table 1. Published and unpublished records of Jaguar (*Panthera onca*) predation on nesting sea turtles across the Americas. Abbreviations are Dc = *Dermochelys coriacea*, Cm = *Chelonia mydas*; Cc = *Caretta caretta*; Lo = *Lepidochelys olivacea*, Ei = *Eretmochelys imbricata*, UN = year and number of predation events unspecified.

<table>
<thead>
<tr>
<th>Country</th>
<th>Years</th>
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<th>Years</th>
<th>Number of turtles predated</th>
<th>Source</th>
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<tr>
<td>Amana Nature Reserve, French Guiana</td>
<td>UN</td>
<td>UN</td>
<td>0</td>
<td>0</td>
<td>Turtle Expert Working Group (2007)</td>
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<tr>
<td>Yalimapo Beach, French Guiana</td>
<td>1983</td>
<td>2</td>
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<td>0</td>
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<td>Galibi Beach, Suriname</td>
<td>1980</td>
<td>0</td>
<td>13</td>
<td>0</td>
<td>Autar (1994)</td>
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<tr>
<td>Galibi Beach, Suriname</td>
<td>1994</td>
<td>0</td>
<td>UN</td>
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<td>Autar (1994)</td>
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<tr>
<td>Corcovado Natl. Park, Costa Rica</td>
<td>1993–1994</td>
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<td>Corcovado Natl. Park, Costa Rica</td>
<td>1996–1998</td>
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<td>0</td>
<td>4 0 Santa Rosa Natl. Park, Ranger logbook (unpublished data)</td>
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<td>19</td>
<td>0</td>
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<td>0</td>
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<td>2016</td>
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<td>Pacuare Nature Reserve, Costa Rica</td>
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<tr>
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<td>2017–2020</td>
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<td>0</td>
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<td>Tortuguero Natl. Park, Costa Rica</td>
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<td>0 0 Carrillo et al. (1994)</td>
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<td>Tortuguero Natl. Park, Costa Rica</td>
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approximately 1.05 km in length and is surrounded by preserved ecosystems characterized by patches of dry forest (deciduous and semi-deciduous), mangroves, lagoons, and two rocky outcrops that delimit the beach. Human activity is regulated by the National Park and also limited by the difficulty in access to the area (Alfaro et al. 2016). Average temperature ranges from 18° C to 36° C, with a mean annual precipitation of 1,500 mm (Janzen 2004).

Data collection and handling.—Between July 2009 and February 2019, we conducted morning surveys (0900 to 1100) to record Jaguar predation events and nocturnal patrols (2000 to 0400) to estimate the size of the local nesting population for each turtle species. Although Olive Ridley Sea Turtles and Green Turtles nest year-round on Nancite Beach, nesting for both species peak from September to November and December to April, respectively. For this reason, we combined data collected between June of one year and May of the following year during eight nesting seasons: 2009–2012 and 2014–2019. We made every effort to conduct both surveys on a daily basis, but funding and logistical limitations prevented daily surveys sporadically during most years, and entirely during two nesting seasons (2012–2013 and 2013–2014).

We documented Jaguar predation on sea turtles by counting sea turtle carcasses along the beach. When a carcass was found, it was examined for evidence of Jaguar predation, such as bite marks on the neck, drag marks in the sand, and Jaguar tracks in proximity (3–5 m) to the carcass. If evidence of predation was found, then we recorded the turtle species and geographic location of the carcass. Although Pumas have been recorded scavenging Jaguar kills at Nancite Beach (Escobar-Lasso et al. 2016a), there is no evidence that Pumas actively kill sea turtles (Fonseca et al. 2018) and therefore all predated carcasses were assumed to be Jaguar kills.

To estimate the size of the local nesting population of Olive Ridley Sea Turtles, we first estimated the total number of nests laid each season (see Fonseca et al. 2009, 2012 for more detailed methodology). When arribadas occurred, we estimated the number of nests based on well-established methodologies, which consisted of setting up 2-m wide transects extending from the vegetation line to the high tide line every 100 m along the beach prior to an arribada (Gates et al. 1996; Valverde and Gates 1999). Along the transects, all turtles with eggs visible in the nest chamber were counted every 2 h for the entire duration of each arribada. The estimated number of clutches deposited during arribadas was then added to the number of solitary nests each season, which were counted individually during nocturnal surveys. We then estimated the number of individuals nesting each season by dividing the annual number of nests by the average clutch frequency for Olive Ridley Sea Turtles (2.21 nests/female/season; van Buskirk and Crowder 1994).

For Green Turtles, we estimated the local nesting population size by tagging all nesting females encountered during the nocturnal surveys with individualized tags (Inconel model 681, National Band and Tag Company, Newport, Kentucky, USA) and counting the total number of individual females encountered each season. We tagged the turtles once they finished laying their eggs and started covering the nest chamber, or when they were encountered returning to the sea. We tagged all turtles in the second proximal scale of each front flipper, after cleaning the scales with an iodine-based disinfectant.

Data analysis and interpretations.—For each season, we estimated Jaguar predation rates for each turtle species by dividing the estimated number of females in the nesting population each year by the number of turtles that were predated on and multiplying by 100 (Arroyo-Arce and Salom-Pérez 2015). To contextualize our results in terms of the effect that Jaguar predation may have on local population persistence, we compared our annual predation rates against an estimated annual mortality rate for adult sea turtles of 0.05 (e.g., each nesting female has a 5% chance of mortality each year of adult life). Because annual survivorship in adult sea turtles is predicted to be high (natural annual survivorship of approximately 0.95; Mazaris et al. 2006), we would expect a predation rate of 5% or greater to detrimentally affect the likelihood of local population persistence over time. Conversely, a predation rate <5% would likely not represent a significant threat to population persistence.

RESULTS

Based on the morning surveys conducted between the 2009–2010 and 2018–2019 nesting seasons (mean survey days per nesting season = 279 ± (standard error) 55 d; Table 2), we documented 171 carcasses of two sea turtle species that demonstrated signs of Jaguar predation (160 Olive Ridley Sea Turtles and 11 Green Turtles). Based on the night surveys, the local nesting population of Olive Ridley Sea Turtles ranged from 10,732 females in the 2009–2010 nesting season to 54,400 females in the 2017–2018 nesting season (mean number of females per nesting season = 32,040 ± 12,149 females; Fig. 2). The local nesting population of Green Turtles ranged from two females in the 2016–2017 nesting season to 26 females in the 2014–2015 nesting season (mean number of females per nesting season = 13.0 ± 8.2 females; Fig. 2).

We found that predation of Olive Ridley Sea Turtles fluctuated over the years (Fig. 2) with the highest number of predation events (52 carcasses) recorded during the 2016–2017 nesting season, representing 0.19% of the
Our results demonstrate that Jaguars annually consumed < 1% of the nesting population of Olive Ridley Sea Turtles (Fig. 2). We found that predation of Green Turtles also fluctuated over the years (Fig. 2), with the highest number of predation events (four carcasses) recorded in both the 2014–2015 and 2015–2016 nesting seasons, representing 15.4% and 28.6% of the nesting population, respectively. We documented no predation events in four nesting seasons.

Our results demonstrate that Jaguars annually consumed between 8.33% to 40% of the local nesting population (Fig. 2).

**Discussion**

The higher frequency of Jaguar predation on Olive Ridley Sea Turtles compared to that of Green Turtles can likely be attributed to the higher abundance and availability of the former, and not to a preference for that species. Olive Ridley Sea Turtles nest in large numbers and exhibit both arribada and solitary nesting behavior.
at Nancite Beach, while Green Turtle abundance is much lower, and nesting is solitary (Plotkin 2007; Fonseca et al. 2009). Thus, the probability of a Jaguar encountering an Olive Ridley Sea Turtle, and therefore predation, is higher in comparison to Green Turtles. A similar density-dependent pattern was observed at Tortuguero National Park, Costa Rica, where Jaguars kill more Green Turtles than Leatherback, Hawksbill, or Loggerhead sea turtles, likely due to their higher abundance and availability throughout the year (Arroyo-Arce and Salom-Pérez 2015; Arroyo-Arce et al. 2017; Arroyo-Arce et al. 2018). Salom (2005) also reported density-dependent predation by Jaguars on Olive Ridley Sea Turtles relative to Green Turtles and Leatherbacks in Corcovado National Park, Costa Rica.

Given that Jaguars can drag the carcasses of all sea turtles except Leatherbacks into the vegetation regardless of their size and weight, and due to the well-known generalist and opportunistic behavior of Jaguars (Rabinowitz and Nottingham 1986), we do not believe that morphological characteristics of sea turtles explain frequency of Jaguar predation in the study area. Given that Jaguars are capable of lifting and carrying the carcasses of smaller Olive Ridley Sea Turtles (carapace length: up to 790 mm; weight: up to 60 kg; Savage 2002) into the vegetation without leaving any identifiable traces, however, a small number of predation events on this species might have been missed. In contrast, predation events by Jaguars on larger Green Turtles (carapace length: 900–1,220 mm; weight: 113–200 kg; Savage 2002) always exhibit clear dragging tracks on the sand or vegetation, making it easy to find their carcasses.

Annual predation rates on Olive Ridley Sea Turtles at Nancite Beach were consistently below 1% of the nesting population. Even though adult sea turtles are predicted to exhibit naturally high annual survivorship (approximately 0.95; Mazaris et al. 2006), a threat that affects < 1% of the annual nesting population is unlikely cause to population decline. Therefore, Jaguar predation likely does not represent a significant threat to the persistence of Olive Ridley Sea Turtles nesting at this regionally important site. Nevertheless, the Olive Ridley Sea Turtle nesting population at Nancite Beach has decreased by approximately 59% from 1971 to 2017 (Valverde et al. 1998; Fonseca et al. 2009; Luis Fonseca et al., unpubl. report). At the same time, it appears that the local Jaguar population is rising. A camera trap study initiated in 2010 identified two individual jaguars in that year, increasing to 11 in 2019, documenting a total of 22 Jaguars between 2010 and 2019 (Luis Fonseca et al., unpubl. report). Despite this apparent increase in local Jaguar abundance, predation rates have remained at < 1% throughout the study period, suggesting that the decline in the local nesting population is likely caused by threats other than Jaguar predation.

One of the main factors that could be contributing to the Olive Ridley Sea Turtle population decline is the low recruitment within the population due to the low hatching success during the years in which the arribadas exceeded 100,000 nests (Valverde et al. 1998; Fonseca et al. 2009). Another significant source of stress for this population is the incidental capture of both juveniles and adults in fishing gear (Plotkin 2007; Mast et al. 2005; Dapp et al. 2013). Dapp et al. (2013) estimated that the Costa Rica longline fisheries caught 699,600 Olive Ridley Sea Turtles (including 92,300 adult females) between 1999 and 2010 in the Central American Pacific, a fishing area adjacent to several arribada beaches including Nancite Beach. Other hazards contributing to its decline are mortality due to take (e.g., human consumption of eggs and meat), pollution and pathogens, climate change, and the degradation or loss of feeding, nesting, migratory, and resting habitats across its geographic range (Cornelius and Robinson 1983; National Research Council 1990; Orrego 2002). These factors all amplify the natural threats already faced by nesting sea turtles, as well as their eggs and hatchlings, such as predation by crustaceans (Ghost Crab, Ocypode quadrata), fish, reptiles (crocodiles, lizards, snakes), birds (seabirds, vultures, pelicans, falcons) and mammals (Coyotes, Raccoons, Procyon lotor, Coatis, Nasua narica, and Jaguars; Hughes and Richard 1974; Cornelius and Robinson 1983; Francia 2004).

Despite the current Olive Ridley Sea Turtle population trend at Nancite Beach, the status of the two East Pacific Regional Management Units (RMUs) suggests a positive trend for the species at a broader population-level (Wallace et al. 2010; Wallace et al. 2011). The East Pacific Ocean Arribada RMU has been categorized as Low Risk-Low Threats, suggesting a positive population trend with low to moderate threats. Further, the East Pacific Ocean Solitary Nesters RMU is considered Low Risk-High Threats, differing from the first in that it is subject to persistent threats that could jeopardize the long-term status of turtles in the RMU. Because both RMUs encompass nesting beaches from Mexico to Peru, and Jaguar predation has only been recorded in a few locations, we would not consider Jaguar predation to be a significant threat for Olive Ridley Sea Turtles at either a local or RMU-wide scale. Further, although the Olive Ridley Sea Turtle population at Nancite Beach has declined (Valverde et al. 1998; Fonseca et al. 2009; Luis Fonseca et al., unpubl. report), there is evidence to suggest that Olive Ridley Sea Turtles could recover if the current hatching rate of the population (hatching success) remains stable, a pattern observed during the last 13 y (Luis Fonseca et al., unpubl. report).

Although the nesting population of Green Turtles...
at Nancite Beach is very small on a regional-scale, the annual predation rate is consistently greater than 5% and occasionally much higher (40%). Because annual survivorship in adult sea turtles is predicted to be high, a predation rate of 5% or greater could detrimentally affect the persistence of Green Turtles nesting at this site over time. In fact, the Green Turtle nesting population at Nancite Beach has fluctuated over the years, characterized by a negative trend (a decline of 32% between 2010 to 2019), while Jaguar numbers have increased in the park over the same years. While the nesting decline could be related to the same threats faced by Olive Ridley Sea Turtles, it cannot be ruled out that Jaguar predation may have, at least in part, contributed to this decline. Despite this negative local trend, the East Pacific Ocean RMU has been categorized as Low Risk-Low Threats (Wallace et al. 2010; Wallace et al. 2011). The Green Turtle nesting population at Nancite Beach is only a small fraction of the broader population, which includes San José Island, Murciélago Archipelago, Costa Rica, one of the most important nesting sites for the East Pacific Ocean RMU (Fonseca et al. 2018). Therefore, based on the current information regarding this predator-prey interaction across the RMUs, we conclude that Jaguars do not constitute a hazard to Green Turtles at a regional level but could influence the recovery of the nesting population at Nancite Beach.

Long-term studies assessing Jaguar predation on sea turtles across the Americas are limited (Arroyo-Arce and Salom-Pérez 2015). Arroyo-Arce and Salom-Pérez (2015) and our findings for Olive Ridley Sea Turtles suggest that although this predator-prey interaction varies between locations, time, and sea turtle species, it is generally not sufficiently high to influence sea turtle populations at local-scales. Conversely, our findings for Green Turtles suggest that Jaguar predation can detrimentally affect the local persistence of small nesting populations when only a few nesting females are predated each year, suggesting that Jaguars may have the capacity to impact sea turtle populations at local-scales. Ortiz et al. (1997) and Ferguson et al. (2000) suggested that White Shark and American Crocodile predation upon sea turtles pose no population-level threat. In contrast, Heithaus et al. (2008) and Pitman and Dutton (2004) suggested that despite low predation rates, predators of adult sea turtles can influence sea turtle populations. Therefore, we consider it important to establish long-term monitoring efforts where this predator-prey interaction occurs to help fill important knowledge gaps, such as the impacts of Jaguars on sea turtle populations and the ecological factors triggering this predator-prey dynamic. For example, sea turtles may be inducing a shift in the spatial and temporal distribution of the Jaguar during the nesting season. A greater knowledge of this subject will improve conservation efforts of both Jaguars and sea turtles in areas were both species coexist.

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