Distribution and hotspots of the feeding areas of jaguars on sea turtles at a national park in Costa Rica

Distribuição e pontos de concentração de áreas de predação de tartarugas marinhas por onças pintadas em parque nacional da Costa Rica

Sergio Escobar-Lasso^{1,2*} biosergiobike@gmail.com

Margarita Gil-Fernández¹

Joel Sáenz¹ jsaenz@una.cr

Eduardo Carrillo-Jiménez¹ eduardo.carrillo.jimenez@una.cr

Grace Wong¹ gwongr@gmail.com

Luis G. Fonseca³ luisfonsecalopez@gmail.com

Diego A. Gómez-Hoyos⁴ biodiego88@gmail.com A poorly described aspect of the trophic relation between sea turtles and jaguars is the distribution and hotspots of the feeding areas of jaguars on the nesting beaches. It is very important to identify the areas where sea turtles are predated because we could concentrate conservation and management efforts in these areas. Therefore, the aim of this work is to describe the spatial distribution and hotspots of the feeding areas of jaguars at Nancite beach, Santa Rosa National Park, Costa Rica. We recorded a total of 76 predated carapaces of sea turtles, of these, 54 (71%) were of *Lepidochelys olivacea* and 22 (29%) of *Chelonia mydas*. Two major feeding hotspots areas were identified within the Nancite beach. Both hotspots are located at the extremes of the beach, one is at the southern edge and the other is at the northern extreme. Human activity and the distribution of nesting turtles influence synergistically to determine the sites where the sea turtles are predated at Nancite beach. Based on the information of predation hotspots, the environmental authorities should regulate the monitoring activities within those areas to avoid interfering with the trophic relation between sea turtles and jaguars.

Keywords: hunting area, jaguar predation, nesting beach, predatory behavior, human-wildlife interactions.

Resumo

Abstract

Um aspecto pouco descrito da relação trófica entre tartarugas marinhas e onças pintadas é a distribuição e os pontos de acesso das áreas de alimentação de onças nas praias de nidificação. Identificar a área onde tartarugas marinhas são predadas é muito importante, porque podemos concentrar os esforços de conservação e de gestão nessas áreas. Portanto, o objetivo deste trabalho é identificar a distribuição espacial e os *hotspots* das áreas de alimentação de onças pintadas na praia Nancite, Parque Nacional de Santa Rosa, Costa Rica. Registramos um total de 76 carapaças predadas de tartarugas marinhas, das quais 54 (71%) eram de *Lepidochelys olivacea* e 22 (29%) de *Chelonia mydas*. Duas grandes áreas de *hotspots* de alimentação foram identificadas na praia Nancite. Ambos os *hotspots* estão localizados nos extremos da praia, sendo um no extremo sul e o outro no extremo norte. A atividade humana e a distribuição de nidificação de tartarugas influenciam sinergicamente para determinar os locais onde as tartarugas marinhas são predadas na praia Nancite. Com base nas informações de *hotspots* de predação, as autoridades ambientais devem regular as atividades de monitoramento nessas áreas, para evitar interferências na relação trófica entre tartarugas marinhas e onças.

¹ Instituto Internacional en Conservación y Manejo de Vida Silvestre. ICOMVIS. Universidad Nacional de Costa Rica. Heredia, 1350-3000, Avenida 1, Calle 9. Apartado Postal: 86-3000, Costa Rica.

² Fundación R.A.N.A (Restauración de Ambientes Neotropicales Alterados). Carrera 15 Calle 12 Norte, Armenia, Quindío, Colombia.

³ Biocenosis Marina, Trinidad de Moravia, San José 1350-3000, Costa Rica.

⁴ Proyecto de Conservación de Aguas y Tierras, ProCAT Internacional/Fundación Sierra to Sea. Carrera 13 No. 96-82, Oficina 205, Bogotá, Colombia. *Corresponding author.

Palavras-chave: área de caça, predação de onças, praia de nidificação, comportamento predatório, interações entre humanos e vida selvagem.

This is an open access article distributed under the terms of the Creative Commons Attribution 4.0 International (CC BY 4.0), which permits reproduction, adaptation, and distribution provided the original author and source are credited.

Introduction

The effect of predators over adult marine turtles has been overlooked because it is difficult to observe and quantify (Heithaus et al., 2008). On the sea, the most common predators of adult sea turtles are sharks and killer whales Orcinus orca (LINNAEUS 1758) (Heithaus et al., 2008). When female adult sea turtles are nesting on the beach, only four different predators have been recorded, namely jaguars Panthera onca (LINNAEUS 1758), American crocodiles Crocodylus acutus (CUVIER 1807), coyotes Canis latrans (SAY 1823), and humans (Ortiz et al., 1997; Drake et al., 2001; Aguirre et al., 2006; Heithaus et al., 2008; Alfaro et al., 2016). Recently, the first record of consumption of sea turtle by a cougar Puma concolor (LINNAEUS 1771) has been reported but it is not clear whether the cougar was acting as a predator or as a scavenger (Escobar-Lasso et al., 2016a).

Humans have been reported to eat all seven species of sea turtles (Aguirre et al., 2006; Dijk et al., 2014). The American crocodile has been recorded preying only on olive ridley sea turtle Lepidochelys olivacea (ESCHSCHOLTZ 1829) (Ortiz et al., 1997). Finally, the jaguar has been recorded killing five species of sea turtles, including green Chelonia mydas (LINNAEUS 1758), olive ridley Lepidochelys olivacea, hawksbill Eretmochelys imbricata (LINNAEUS 1766), loggerhead sea turtle Caretta caretta (LINNAEUS 1758), and leatherback Dermochelys coriacea (VANDELLI 1761) sea turtles (Fretey, 1977; Autar, 1994; Carrillo et al., 1994; Chinchilla, 1997; Tröeng, 2000; Heithaus et al., 2008; Veríssimo et al., 2012; Keeran, 2013; Arroyo-Arce et al., 2014; Cuevas et al., 2014; Arroyo-Arce and Salom-Pérez, 2015; Guilder et al., 2015; Alfaro et al., 2016; Arroyo-Arce et al., 2017).

It is important to highlight that the jaguar and the American crocodile (Crocodylus acutus) are the only predators recorded in Nancite beach capable to kill sea turtles (Cornelius, 1986; Carrillo et al., 1994; Ortiz et al., 1997; Figure 1). However, predation events by American crocodiles on sea turtles are extremely rare in this beach (Ortiz et al., 1997). Sea turtles are important food sources for jaguars because they are easy prey and they represent a big amount of biomass (Veríssimo et al., 2012; Arroyo-Arce and Salom-Pérez, 2015; Guilder et al., 2015). Additionally, they can be key resources when other prey availability is low (Veríssimo et al., 2012). Recently, it has been discovered that many species of vertebrate scavengers could be indirectly benefited by the predator-prey relationship between jaguars and sea turtles (Escobar-Lasso et al., 2016b). Therefore, the sea turtles could also be key resources for scavengers in periods when the availability of other types of carcasses is low (Escobar-Lasso et al., 2016b).

The trophic relation between sea turtles and jaguars is one of the most interesting and controversial because it

involves six species threatened with extinction (Veríssimo et al., 2012; Arroyo-Arce et al., 2017). On the other hand, sea turtles and jaguars are widely recognized as conservation flagship species (Caro et al., 2004; Eckert and Hemphill, 2005) and large-scale projects have been developed to conserve them (Bjorndal et al., 1999; Ceballos et al., 2002). Historically, four species have been recorded nesting on Nancite beach, namely Lepidochelys olivacea, Chelonia mydas, Eretmochelys imbricata and Dermochelys coriacea (Cornelius, 1986; Fonseca et al., 2009). However, D. coriacea and E. imbricata are extremely rare and their occurrence in Nancite is very low (Cornelius, 1986). It must be highlighted that L. olivacea has been catalogued as vulnerable and C. mydas as endangered by the IUCN, also, these species are decreasing worldwide, according to their population trend (Seminoff, 2004; Abreu-Grobois and Plotkin, 2008). In regard to the jaguar, this species is considered to be near threatened by the IUCN, and its populations are also decreasing (Caso et al., 2008). For their critical state, knowledge about these species and its predatory interactions is imperative.

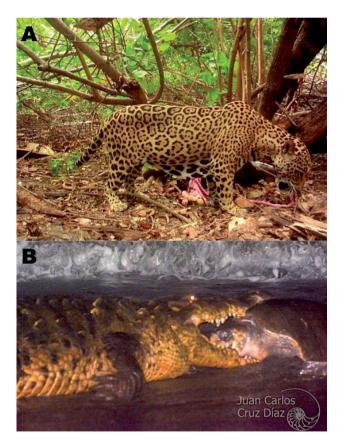


Figure 1. Jaguar (*Panthera onca*) and American crocodile (*Crocodylus acutus*) feeding on a sea turtle on Nancite Beach, Santa Rosa National Park, Costa Rica. Photos by Luis G. Fonseca (A) and Juan Carlos Cruz Díaz.

Sergio Escobar-Lasso, Margarita Gil-Fernández, Joel Sáenz, Eduardo Carrillo-Jiménez, Grace Wong, Luis G. Fonseca, Diego A. Gómez-Hoyos

The knowledge of the ecological aspects of jaguar-sea turtle relationships may contribute to their conservation and to take management decisions (Alfaro *et al.*, 2016). The temporal and spatial trends of jaguar predation on turtles have been recently studied (Veríssimo *et al.*, 2012), as well as carcass utilization rates (Tröeng, 2000; Guilder *et al.*, 2015; Alfaro *et al.*, 2016), the intraspecific interactions between jaguars (Escobar-Lasso *et al.*, 2016c), the influence of the scavengers on the feeding behavior of the jaguar on sea turtles (Escobar-Lasso *et al.*, 2016b) and the impact on sea turtle populations (Arroyo-Arce and Salom-Pérez, 2015). However, a poorly described aspect is the distribution of the feeding areas of the jaguar on sea turtles on its nesting beaches (Veríssimo *et al.*, 2012; Arroyo-Arce and Salom-Pérez, 2015; Alfaro *et al.*, 2015; Alfaro *et al.*, 2016).

There have been reported predations of sea turtles by jaguars in eight beaches throughout America (Fretey, 1977; Autar, 1994; Carrillo et al., 1994; Keeran, 2013; Cuevas et al., 2014; Guilder et al., 2015; Alfaro et al., 2016; Arroyo-Arce et al., 2016), but in only two beaches, both in Costa Rica, the distribution and hotspots of the feeding areas of jaguars on sea turtles were reported: (a) Tortuguero National Park (Veríssimo et al., 2012; Arroyo-Arce and Salom-Pérez, 2015) and (b) Naranjo beach, Santa Rosa National Park (Alfaro et al., 2016). These works have found that the distribution of the feeding areas varies spatially and there are distinct hotspots across the beaches. Identify the distribution and hotspots of the feeding areas of the jaguars on sea turtles is very important because all conservation and management efforts should be concentrated in these areas to maintain the trophic relationship between jaguars and sea turtles. Therefore, the aims of this work are: (a) to document the number of predation events of jaguars on sea turtles at Nancite beach and (b) to describe the spatial distribution and hotspots of the feeding areas of jaguars on sea turtles at Nancite beach, Santa Rosa National Park, Costa Rica.

Materials and methods

Study site

Santa Rosa National Park is located in the Guanacaste Province, Northwestern Pacific coast of Costa Rica. Santa Rosa comprehends one of the best-preserved dry forests of Central America. This National Park has an extension of 38,628 ha and it is within a block of 163,000 ha of protected land within the Guanacaste Conservation Area. In this park there are several important sea turtles nesting beaches (e.g. Naranjo, Colorada, Nancite, Isla San Jose, Potrero Grande, among others). One of the most important nesting beaches for sea turtles is Nancite (Cornelius, 1986), located in the Southwestern part of Santa Rosa National Park (10°48'N and 85°39'W; Figure 2); it has a length of

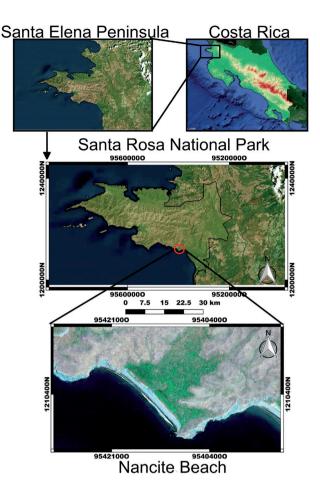


Figure 2. Location of Nancite Beach, Santa Rosa National Park, Guanacaste Province, Costa Rica.

approximately 1050 m and it preserves mainly coastalmarine ecosystems (besides mangroves, lagoons and dry deciduous and semi-deciduous forests).

Nancite beach has been fully protected from intrusive human activities, including tourism and it supports a well preserved wild ecosystem (Figure 3). This beach is important because is one of the few places in the world that presents the olive ridley arribada phenomenon (Cornelius, 1986; Fonseca *et al.*, 2009). This phenomenon consists of the massive synchronous nesting of hundreds or thousands of olive ridley over a few consecutive nights (Cornelius, 1986; Bernardo and Plotkin, 2007; Fonseca *et al.*, 2009). This phenomenon also occurs in other beach in Costa Rica (Ostional beach) and some beaches in Mexico, India, Nicaragua and Panama (Fonseca *et al.*, 2009).

Methods

The distribution and hotspots of the feeding sites of jaguars on sea turtles was assessed through diurnal surveys. These surveys were made by Escobar-Lasso between October 1st 2015 and February 29th 2016 at Nancite beach. It is noteworthy that during the performance of this investigation the area was presenting the climate conditions called "El niño". During these surveys we look for carapaces of sea turtles (Figure 4) inside the beach vegetation and nearby forests (Figure 3). The following variables were recorded: (i) the species of sea turtle, (ii) the geographic location (coordinates), and (iii) the distance in meters that the jaguar dragged the sea turtle carcasses from the beach to the forest (see Appendix 1). In order to avoid duplication of carcasses, we mark every carapace with red painting when its location was recorded. Therefore, when a carapace was found it was examined to identify jaguar predation signals (e.g. bite marks on the anterior part of



Figure 3. Nancite Beach, Santa Rosa National Park, Guanacaste Province, Costa Rica. Photo by Sergio Escobar-Lasso.

carapace; Figures 3 and 4). We assume that every carapace found in the beach vegetation and nearby forest corresponds to a predation event by the jaguar.

The identification of the species of sea turtle was based on its carapace (Cornelius, 1986). The olive ridley sea turtle has ovate shaped carapace, 5 to 9 lateral scales and an average length of 65 cm (Figure 4a). The green sea turtle has a drop shaped carapace, 4 lateral scales and an average length of 80 cm (Figure 4b).

The distribution and hotspots of the feeding sites of jaguars on sea turtles were computed and mapped using the plugin Heatspots of Qgis version 2.14. The hotspots size was calculated using the plugin Measuring areas of Qgis version 2.14. We used t-Student test to evaluate the differences in distance of drag of the carcasses of green versus olive ridley sea turtles. The statistical analysis was performed using R language with Rcmdr interface (Fox, 2005) and the graphics were made using the ggplot2 package (Wickham, 2009).

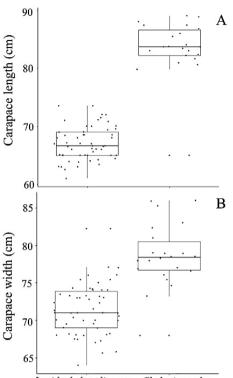
Results

We recorded a total of 76 carapaces of sea turtles predated by jaguars, 54 (71 %) of which were on olive ridley sea turtles and 22 (29%) on green sea turtles. The carapace of the olive ridley sea turtles presented a length of 67.1 \pm 2.94 cm (61-73.5 m) and a width of 71.4 \pm 3.41 cm (64-82.2 m) (Figure 5). The green turtle carapaces had a length of 83.5 \pm 4.92 cm (65-89 m) and a width of 78.6 \pm 4.23 cm (68-86 m) (Figure 5). The jaguars dragged the sea turtles' carcasses from the beach to the forest 78.39 m in average (\pm 77.46 m, range = 3-336 m). For the green sea turtles the average distance of drag was 60.72 \pm 56.69 m (3-220 m) and for olive



Figure 4. Carapaces of sea turtles predated by jaguars (*Panthera onca*) at Nancite beach, Santa Rosa National Park, Costa Rica. (A) Carapace of olive ridley sea turtle (*Lepidochelys olivacea*) and (B) carapace of green sea turtle (*Chelonia mydas*). Note the bite marks of the jaguar in the fore part of the sea turtles' carapaces.

ridley sea turtles it was of 85.59 ± 83.88 m (8-336 m). However, there were no statistical differences in the distance of drag between both species (t = 1.49, p = 0.140).



Lepidochelys olivacea Chelonia mydas

Figure 5. Differences between the length (A) and width (B) of the carapaces of olive ridley (*Lepidochelys olivacea*) and green (*Chelonia mydas*) sea turtles, which were killed by jaguars (*Phantera onca*) and were found in the surrounding vegetation of Nancite beach, Santa Rosa National Park, Costa Rica.

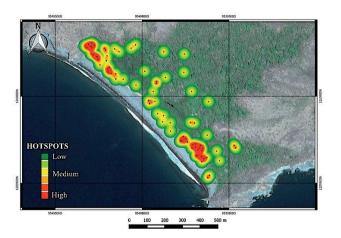


Figure 6. Distribution and hotspots of the predation events by jaguars (*Panthera onca*) on sea turtles at Nancite beach, Santa Rosa National Park, Costa Rica.

By analyzing the distribution and hotspots of the feeding areas of jaguars on olive ridley and green sea turtles, we found spatial variation and separated feeding hotspots areas across the Nancite beach (Figure 6). Furthermore, two major hotspots of feeding were identified within the study area. The hotspots are located on the southern and northern extremes of the beach (Figure 6). The southern hotspot is slightly greater (19 events; 837 m²) compared with the northern hotspot (11 events; 570 m²).

Although the numbers of predation events were different for green and olive ridley sea turtles, the distribution and hotspots of the feeding areas of jaguars were similar; therefore, two major feeding hotspots areas were identified regardless of the species (Figure 7). In the species-specific distribution, for green sea turtles the southern hotspot is slightly greater (6 events; 600m²) and denser compared with the northern hotspot (two events; 50m²) (see Figure 7a). On the contrary in olive ridley sea turtles the northern hotspot is slightly greater (17 events) but highly dispersed

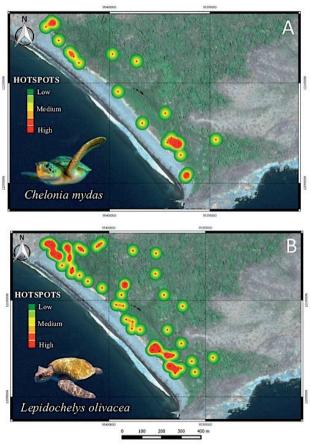


Figure 7. Distribution and hotspots of the predation events by jaguars (*Panthera onca*) on green sea turtles (*Chelonia mydas*) (A) and olive ridley sea turtles (*Lepidochelys olivacea*) (B) at Nancite beach, Santa Rosa National Park, Costa Rica.

(480 m²) compared with the southern hotspot (13 events) that is less dispersed (410 m²) (Figure 7b).

Discussion

Our results show that the jaguars dragged the sea turtle carcasses from the beach to the forest a maximum distance of 336 m. Alfaro et al. (2016) found that the jaguars dragged the carcasses a maximum distance of 1025 m on Naranjo beach. It is believed that the jaguars drag the sea turtle carcasses into dense vegetation as an attempt to conceal them from scavengers (Guilder et al., 2015). The green sea turtle is heavier (70-125 kg) compared to olive ridley sea turtle (35-45 kg) (Cornelius, 1986), in any case, we did not find statistical differences in the distance of drag among green and olive ridley sea turtles. It is possible that green sea turtles are not heavy enough to hold the jaguar from harrow them and for this reason no differences were found. Apart from the scavengers, the dragging distance could be related to the vegetation cover type, where less dense cover demands a longer distance of dragging to conceal the carcass. Even when vegetation is highly homogeneous along the beach, studies addressing this variable could reveal more about dragging distance.

Our results demonstrate that Nancite beach is not used uniformly for feeding by jaguars. The distribution of the feeding areas varies spatially, and it reveals distinct hotspots across Nancite beach. Similar results also have been reported in Tortuguero National Park (Veríssimo et al., 2012; Arroyo-Arce and Salom-Pérez, 2015) and in Naranjo beach, Santa Rosa National Park (Alfaro et al., 2016). For jaguars, the three main factors that determine the distribution and hotspots of the feeding areas are: (a) distribution of the human activity along the beach, (b) distribution of the nesting female turtles along the beach, and (c) interactions and territorial behaviors among jaguars (Veríssimo et al., 2012; Arroyo-Arce and Salom-Pérez, 2015; Alfaro et al., 2016). These three factors may act independently or synergistically depending on the particular circumstances for each beach (Veríssimo et al., 2012; Arroyo-Arce and Salom-Pérez, 2015).

Several studies have recorded that the jaguar tends to avoid human-dominated areas (Cullen *et al.*, 2013). Therefore, it is expected that the core areas of jaguar activity and its feeding hotspots areas would be located away from infrastructure and human presence (Arroyo-Arce and Salom-Pérez, 2015). For example, in Tortuguero beach the sea turtle feeding hotspots are located in the farther extreme from the Tortuguero village (Veríssimo *et al.*, 2012; Arroyo-Arce and Salom-Pérez, 2015). Similarly, Alfaro *et al.* (2016) recorded that the feeding areas are located far from camping sites (which have the higher tourist concentration). At Nancite beach the tourism is strictly prohibited, however the beach is open to scientific research. During most of the year there are groups of researchers and volunteers monitoring the nesting of sea turtles. These groups are composed in certain occasions of up to 25 people, who live on the biological station of Nancite and patrol the beach all nights, time during which the jaguars are in activity and feed on sea turtles.

The human activity restricts the feeding hotspots areas of the jaguars at Tortuguero beach (Veríssimo et al., 2012; Arroyo-Arce and Salom-Pérez, 2015) and at Naranjo beach (Alfaro et al., 2016). We believe that the negative effect of human activity could be higher in Nancite considering that this beach has a length of only 1050 m, which is much smaller, compared to Tortuguero (with 29 km of length) and Naranjo (with 6 km of length) beaches. The areas without human presence are less in Nancite due to its small size. Our results suggest that human activity could restrict the sea turtle predation area in Nancite because the main path that leads to the beach and the biggest infrastructure of the station are located in the center of the beach. Therefore, the activity of researchers and volunteers is concentrated in the center of the beach, which could explain the fact that sea turtle predation hotspots are located on the southern and northern extremes, and not in the center of the beach.

In addition to human activity, the spatial distribution of the nesting sea turtles along the beach is other factor that could also be affecting the spatial arrangement of jaguar feeding areas in Nancite beach. Interestingly, at Naranjo and Tortuguero, the areas with more nesting sea turtles are also the zones with less human activity, and these concentrate the sea turtle feeding hotspots (Veríssimo et al., 2012; Arroyo-Arce and Salom-Pérez, 2015; Alfaro et al., 2016). We find something similar on Nancite beach. The areas of greatest sea turtle nesting in Nancite are in the central and northern part of the beach (Fonseca et al., 2009). Hence, in the predation hotspot located in the north of Nancite (Figure 7) the pattern recorded in Naranjo (Alfro et al., 2016) and Tortuguero (Arroyo-Arce and Salom-Pérez, 2015) is repeated. However, there is a high human activity in the center of the beach at some point of the year, and it might be possible that this prevents the jaguar from hunting. This allows the formation of a hotspot in the southern part of the beach, even when this area has less sea turtle nesting compared to the central and northern areas of the beach. This suggests that both human activity and the distribution of nesting turtles influence synergistically to determine the sea turtle hunting area and the sea turtle predation hotspots in Nancite beach. However, other factors specific to the habitat may also determine the size and distribution of the feeding sites. Habitat variables have not been evaluated in this study, nor in previous works (Verissimo et al., 2012, Arroyo-Arce and Salon-Pérez, 2015, Alfaro et al., 2016).

Throughout America, the jaguar has been recorded killing nesting sea turtles (Wyneken *et al.*, 2013); nevertheless, there are few studies that follow the rates of predation Sergio Escobar-Lasso, Margarita Gil-Fernández, Joel Sáenz, Eduardo Carrillo-Jiménez, Grace Wong, Luis G. Fonseca, Diego A. Gómez-Hoyos

events. In Suriname, jaguars killed at least 82 green turtles over eleven years (Autar, 1994). Moreover, most of the knowledge about the predator-prey relation between jaguars and sea turtles has been derived from studies in Costa Rica. These studies have been conducted on four sea turtle nesting beaches, at three National Parks: Tortuguero (Tröeng, 2000; Veríssimo *et al.*, 2012; Arroyo-Arce *et al.*, 2014; Arroyo-Arce and Salom-Pérez, 2015; Guilder *et al.*, 2015), Corcovado (Carrillo *et al.*, 1994; Chinchilla, 1997) and Santa Rosa (Carrillo *et al.*, 1994; Alfaro *et al.*, 2016). All these areas have high tourism activities and research with volunteers.

Traces of wild carnivores are scarce where people are allowed (Coghlan, 2008). Ideally, the research activities should not interfere in the trophic relations between jaguars and sea turtles. In this sense, to identify the sea turtle feeding hotspots is very important to guide management actions and prevent or mitigate all possible threats that may alter the trophic relationship between jaguars and sea turtles. Therefore, the environmental authorities of Nancite, based on the information of the feeding hotspots, should apply strategies to protect the trophic relations within those key zones. In this sense, research activities could be reorganized in order to be extra-cautious with these ecological interactions. A management option could be a different distribution of people in night patrols; they could wait at stable sites as far as possible from the nesting hotspots. Also, there should be less movement across the beach to avoid disturbing the jaguars.

Within Santa Rosa National Park there are several important sea turtles nesting beaches where jaguars have been recorded preying sea turtles (e.g. Naranjo, Colorada, Nancite, Potrero Grande). The sea turtle predation hotspots have been recorded only in Naranjo (Alfaro *et al.*, 20016) and Nancite (this work). Therefore, additional research must be done at Potrero Grande and Colorada beaches to document the sea turtle predation hotspots.

Acknowledgements

We thank to the anonymous reviewers for providing valuable comments. This work was made possible by a graduate scholarship from the U.S. Fish and Wildlife Service to Sergio Escobar-Lasso, Hansel Herrera and Margarita Gil-Fernández.

References

ABREU-GROBOIS, A; PLOTKIN, P. 2008. *Lepidochelys olivacea*. The IUCN Red List of Threatened Species.

http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T11534A3292503.en AGUIRRE, A.A.; GARDNER, S.C.; MARSH, J.C.; DELGADO, S.G.; LIMPUS, C.J.; NICHOLS, W.J. 2006. Hazards associated with the consumption of sea turtle meat and eggs: A review for health care workers and the general public. *EcoHealth*, **3**(3):141-153.

https://doi.org/10.1007/s10393-006-0032-x

ALFARO, L.D.; MONTALVO, V.; GUIMARAES, F.; SAENZ, C.; CRUZ, J.; MORAZAN, F.; CARRILLO, E. 2016. Characterization of attack events on sea turtles (*Chelonia mydas* and *Lepidochelys olivacea*) by jaguar (*Panthera onca*) in Naranjo sector, Santa Rosa National Park, Costa Rica. *International journal of conservation science*, **7**(1):101-108. ARROYO-ARCE, S.; GUILDER, J.; SALOM-PÉREZ, R. 2014. Habitat features influencing jaguar *Panthera onca* (Carnivora: Felidae) occupancy in Tortuguero National Park, Costa Rica. *Revista de Biología Tropical*, **62**(4):1449-1458. https://doi.org/10.15517/rbt.v62i4.13314

ARROYO-ARCE, S.; SALOM-PÉREZ, R. 2015. Impact of Jaguar *Panthera onca* (Carnivora: Felidae) predation on marine turtle populations in Tortuguero, Caribbean coast of Costa Rica. *Revista de Biología Tropical*, **63**(3):815-825. https://doi.org/10.15517/rbt.v63i3.16537

ARROYO-ARCE, S.; THOMSON, I.; FERNÁNDEZ, C.; SALOM-PÉREZ, R. 2016. First record of a marine turtle predated by a jaguar in Pacuare Nature Reserve, Costa Rica. *Cat News*, **64**:6-7.

ARROYO-ARCE, S.; THOMSON, I.; HARRISON, E.; WILMOTT, S.; BAKER, G. 2017. First record of jaguar (*Panthera onca*) predation on a loggerhead sea turtle (*Caretta caretta*) in Tortuguero National Park, Costa Rica. *Herpetology Notes*, **10**:17-18.

AUTAR, L. 1994. Sea turtles attacked and killed by jaguars in Suriname. *Marine Turtle Newsletter*, **67**:11-12.

BERNARDO, J.; PLOTKIN, P.T. 2007. An evolutionary perspective on the arribada phenomenon and reproductive behavioral polymorphism of olive ridley sea turtles, (*Lepidochelys olivacea*). *In*: P.T. PLOTKIN (ed.), *Biology and Conservation of Ridley sea Turtles*. Baltimore, Johns Hopkins University Press, p. 59-87.

BJORNDAL, K.A.; WETHERALL, J.A.; BOLTEN, A.B.; MORTIM-ER, J.A. 1999. Twenty-six years of green turtle nesting at Tortuguero, Costa Rica: an encouraging trend. *Conservation Biology*, **13**(1):126-134. https://doi.org/10.1046/j.1523-1739.1999.97329.x

CARO, T.; ENGILIS, J.R.; FITZHERBERT, E.; GARDNER, T. 2004. Preliminary assessment of the flagship species concept at a small scale. *Animal Conservation*, **7**(1):63-70.

https://doi.org/10.1017/S136794300300115X

CARRILLO, E.; MORERA-AVILA, R.A.; WONG-REYES, G. 1994. Depredación de tortuga lora (*Lepidochelys olivacea*) y de tortuga verde (*Chelonia mydas*) por el jaguar (*Panthera onca*). *Vida Silvestre Neotropical*, **3**(1):48-49.

CASO, A.; LOPEZ-GONZALEZ, C.; PAYAN, E.; EIZIRIK, E.; DE OLIVEIRA, T.; LEITE-PITMAN, R.; KELLY, M.; VALDERRAMA, C. 2008. *Panthera onca*. The IUCN Red List of Threatened Species.

http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T15953A5327466.en

CEBALLOS, G.; CHÁVEZ, C.; RIVERA, A.; MANTEROLA, C.; WALL, B. 2002. Tamaño poblacional y conservación del jaguar en la reserva de la biosfera Calakmul, Campeche, México. *In*: R.A. ME-DELLÍN (ed.), *El jaguar en el nuevo milenio*. Mexico DF, Fondo de cultura económica, UNAM, p. 403-417.

CHINCHILLA, F.A. 1997. La dieta del jaguar (*Panthera onca*), el puma (*Felis concolor*) y el manigordo (*Felis pardalis*) en el Parque Nacional Corcovado, Costa Rica. *Revista de Biologia Tropical*, **45**:1223-1229.

COGHLAN, A. 2008. Can tourism and wildlife ever mix? *New Scientist*, **199**:10.

CORNELIUS, S.E. 1986. *The sea turtles of Santa Rosa National Park*. San José, Fundación de Parques Nacionales, 64 p.

CUEVAS, E.; FALLERM, J.C.; ANGULO, A.; ANDRADE, M.; PUC, R.A.; GONZÁLEZ, B.I. 2014. Marine turtles and jaguars: two mystical species coexisting on the coast of Quintana Roo, México. *Biodiversitas*, **114**:13-16.

CULLEN, L.; SANA, D.A.; LIMA, F.; ABREU, K.C.; UEZU. A. 2013. Selection of habitat by the jaguar, *Panthera onca* (Carnivora: Felidae), in the upper Paraná River, Brazil. *Zoologia* (*Curitiba*), **30**(4):379-387. https://doi.org/10.1590/S1984-46702013000400003

DIJK, P.P.; IVERSON, J.B.; RHODIN, A.G.J.; SHAFFER. H.B.; BOUR, R. 2014. Turtles of the world: Annotated Checklist of Taxonomy, Syn-

onymy, Distribution with Maps, and Conservation Status. *Chelonian Research Monographs*, **5**:329-479.

DRAKE, D.D.; HAGERTY, A.M.; BEHM, E.J.; GOLDENBURG, J.S. 2001. *Lepidochelys olivacea* (Olive Ridley Sea Turtle) Predation. *Herpetological Review*, **32**:104.

ECKERT, K.L.; HEMPHILL, A.H. 2005. Sea turtles as flagships for protection of the wider Caribbean region. *Maritime Studies*, **3**(2):119-143.

ESCOBAR-LASSO, S.; FONSECA, L.G.; GIL-FERNÁNDEZ, M.; VILLACHICA, W.N.; ARROYO-ARCE, S.; THOMSON, I.; SÁENZ, J. 2016a. First record of consumption of olive ridley sea turtle by a cougar. *Cat News*, **64**:4-5.

ESCOBAR-LASSO, S.; GIL-FERNANDEZ, M.; SÁENZ, J.; CARRIL-LO-JIMÉNEZ, E.; WONG, G.; FONSECA, L.G. 2016b. Inter-trophic food provisioning between sea and land: the jaguar (*Panthera onca*) as provider of sea turtle carcasses to terrestrial scavengers. *International journal of conservation science*, **7**(4):1081-1094.

ESCOBAR-LASSO, S.; GIL-FERNÁNDEZ, M.; HERRERA, H.; FON-SECA, L.G.; CARRILLO-JIMÉNEZ, E.; SÁENZ, J.; WONG, G. 2016c. Scavenging on sea turtle carcasses by multiple jaguars in Northwestern Costa Rica. *Therya*, **7**(2):231-239.

https://doi.org/10.12933/therya-16-380

FONSECA, L.G.; MURILLO, A.G.; GUADAMÚZ, L.; SPÍNOLA, R.M.; VALVERDE, R. 2009. Downward but stable trend in the abundance of arribada Olive Ridley sea Turtle (*Lepidochelys olivacea*) at Nancite Beach, Costa Rica (1971-2007). *Chelonian Conservation and Biology*, 8(1):19-27. https://doi.org/10.2744/CCB-0739.1

FOX, J. 2005. The Rcommander: A Basic Statistics Graphical User Interface to R. *Journal of Statistical Software*, **14**:1-42.

https://doi.org/10.18637/jss.v014.i09

FRETEY, J. 1977. Cuases de motalite des tortues luth adults (*Dermochelys coriacea*) sur le littoral guayanais. *Courrier de la Nature*, **52**:257-266.

GUILDER, J.; BARCA, B.; ARROYO-ARCE, S.; GRAMAJO, R.; SA-LOM-PÉREZ, R. 2015. Jaguars (*Panthera onca*) increase kill utilization rates and share prey in response to seasonal fluctuations in nesting green turtle (*Chelonia mydas mydas*) abundance in Tortuguero National Park, Costa Rica. *Mammalian Biology*, **80**(2):65-72.

https://doi.org/10.1016/j.mambio.2014.11.005

HEITHAUS, M.R.; WIRSING, A.J.; THOMSON, J.A.; BURKOLDER, D.A. 2008. A review of lethal and non-lethal effects of predators on adult marine turtles. *Journal of Experimental Marine Biology and Ecology*, **356**(1):43-51. https://doi.org/10.1016/j.jembe.2007.12.013

KEERAN, D. 2013. Jaguars killing endangered marine turtles almost for fun. Available at: http://www.kaieteurnewsonline.com/2013/07/14/ jaguars-killing-endangered-marine-turtles-almost-for-fun-conservation-ist/. Accessed on: April 3rd, 2016.

ORTIZ, R.M.; PLOTKIN, P.T.; OWENS, D.W. 1997. Predation on olive ridley sea turtles (*Lepidochelys olivacea*) by the American crocodile (*Crocodylus acutus*) at Playa Nancite, Costa Rica. *Chelonian Conservation Biology*, **2**:585-587.

SEMINOFF, J.A. 2004. *Chelonia mydas*. The IUCN Red List of Threatened Species.

http://dx.doi.org/10.2305/IUCN.UK.2004.RLTS.T4615A11037468.en

TROËNG, S. 2000. Predation of green (*Chelonia mydas*) and leatherback (*Dermochelys coriacea*) turtles by jaguar (*Panthera onca*) at Tortuguero National Park, Costa Rica. *Chelonian Conservation and Biology*, **3**(4):751-753.

VERÍSSIMO, D.; JONES, D.A.; CHAVERRI, R.; MEYER. S.R. 2012. Jaguar *Panthera onca* predation of marine turtles: conflict between flagship species in Tortuguero, Costa Rica. *Oryx*, **46**(3):340-347. https://doi.org/10.1017/S0030605311001487

WICKHAM, H 2009. Elegant Graphics for Data Analysis. EE.UU, Springer, 210 p.

WYNEKEN, J.; LOHMANN, K.J.; MUSICK, J.A. 2013. The Biology of Sea Turtles. Costa Rica, CRC Press, vol. 3, 475 p. https://doi.org/10.1201/b13895

Submitted on May 11, 2016 Accepted on December 8, 2016 Sergio Escobar-Lasso, Margarita Gil-Fernández, Joel Sáenz, Eduardo Carrillo-Jiménez, Grace Wong, Luis G. Fonseca, Diego A. Gómez-Hoyos

Appendix 1. Records of carapaces of sea turtles found in the beach vegetation and nearby forest at Nancite beach, Santa Rosa National Park, Costa Rica. Each carapace corresponds to an independent predation event by the jaguars.

Number	Species	Carapace Length	Carapace width	Y	х	Distance from the beach
1	olive	65,1	68,2	10,80755065	-85,70221723	24
2	green	65,0	68,0	10,80746176	-85,70212001	20
3	olive	64,4	67,5	10,80762565	-85,70204501	42
4	olive	65,0	68,2	10,80752565	-85,70193389	26
5	olive	65,6	67,5	10,80746453	-85,70186167	37
6	green	89,0	85,3	10,80768676	-85,70188112	52
7	green	83,0	78,0	10,80758676	-85,70174501	56
8	olive	63,4	65,6	10,80700065	-85,70160612	30
9	olive	66,5	74,0	10,8074312	-85,70123112	95
10	olive	63,9	70,6	10,80704787	-85,70108945	77
11	olive	71,5	82,2	10,80680342	-85,70112278	56
12	olive	69,4	72,8	10,8074062	-85,70069778	136
13	olive	64,2	71,0	10,80647009	-85,70097278	40
14	olive	62,5	67,3	10,80743676	-85,699845	200
15	olive	66,5	72,3	10,80613676	-85,70063945	38
16	olive	70,8	71,3	10,80586453	-85,70025334	28
17	olive	63,0	73,0	10,80556453	-85,699595	43
18	green	84,0	79,0	10,80626731	-85,69913667	138
19	olive	65,0	68,1	10,80573953	-85,69852278	117
20	olive	67,0	71,5	10,80523953	-85,69869778	83
21	olive	61,0	65,8	10,80478675	-85,69893945	29
22	olive	68,0	69,5	10,80473398	-85,69861723	52
23	olive	73,5	74,3	10,80401453	-85,69817	41
24	olive	68,0	74,2	10,8036562	-85,69782556	44
25	olive	66,6	71,0	10,80523953	-85,69671722	254
26	green	83,7	78,9	10,80366731	-85,69678667	128
27	olive	69,5	73,3	10,80295064	-85,69714778	47
28	olive	68,5	75,4	10,80272842	-85,69721445	21
29	olive	71,1	73,2	10,80283953	-85,69702278	46
30	olive	66,2	70,4	10,80267286	-85,69693389	42
31	green	86,0	81,0	10,80237009	-85,696695	33
32	olive	68,5	75,4	10,8025312	-85,69664222	44
33	olive	65,0	70,0	10,8019812	-85,69641167	25
34	green	83,7	78,3	10,80257564	-85,69651167	63
35	olive	65,0	68,0	10,80241731	-85,69651167	50
36	green	86,8	83,0	10,80227842	-85,69637833	47
37	green	83,7	78,9	10,80237842	-85,69631167	62
38	olive	64,0	70,0	10,80249231	-85,69625611	74
39	olive	66,0	70,0	10,80302286	-85,69591445	142
40	green	83,0	78,0	10,80235064	-85,69617278	70
41	green	88,0	86,0	10,80182009	-85,69608945	40
42	olive	71,0	77,0	10,80221175	-85,69542556	128
43	green	87,4	82,3	10,80098397	-85,695795	30
44	olive	65,0	68,0	10,80237564	-85,69443944	225
45	olive	69,0	74,0	10,80715898	-85,70191167	16
46	olive	66,0	69,0	10,8071062	-85,70180334	28
40	olive	68,4	72,4	10,8071002	-85,70159778	32
47 48		80,6	72,4 77			32 27
	green			10,80686453	-85,70154778	
49	olive	66,0	70,0	10,80734231	-85,70116445	95
50	olive	63,0	67,0	10,80658953	-85,70145334	18
51	green	82,2	76,6	10,80635898	-85,70105334	27
52	olive	67,0	73,0	10,80623398	-85,70102834	20

Appendix 1. Continuation.

Number	Species	Carapace Length	Carapace width	Y	Х	Distance from the beach
53	green	80,9	76,1	10,80615342	-85,70087556	25
54	olive	67,0	71,0	10,8072562	-85,70046723	145
55	green	85,5	78,5	10,80595064	-85,69806723	182
56	olive	72,0	76,0	10,80565342	-85,69854778	108
57	green	81,6	74,6	10,80462009	-85,698895	15
58	olive	68,0	69,5	10,80412009	-85,69847834	12
59	olive	73,5	74,3	10,80370342	-85,69821445	8
60	green	87,4	76,9	10,80322564	-85,69781167	3
61	olive	66,6	71,0	10,8027312	-85,69728667	12
62	olive	63,8	64,0	10,80364509	-85,69656167	140
63	olive	69,0	71,0	10,80199231	-85,69648667	16
64	green	83,4	78,5	10,80224786	-85,69618389	63
65	olive	63,0	73,0	10,80193397	-85,69622	35
66	olive	70,0	73,5	10,80167009	-85,696195	21
67	olive	65,0	68,1	10,80188397	-85,69592556	62
68	green	82,3	75,4	10,80086453	-85,69588111	22
69	olive	72,0	76,0	10,80760342	-85,69961723	233
70	green	79,8	73,2	10,80587842	-85,70063945	13
71	olive	70,0	75,0	10,80725898	-85,69815889	283
72	olive	68,5	77,1	10,80713676	-85,69709222	336
73	olive	70,1	73,3	10,80621176	-85,69712	279
74	olive	67,1	74,0	10,80472287	-85,69584778	278
75	green	88,9	85,9	10,80250064	-85,69452278	220
76	olive	65,0	69,0	10,80172009	-85,69527278	109

Notes: olive = Olive ridley sea turtle (Lepidochelys olivacea), green = Green sea turtle (Chelonia mydas).