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Influence of sea turtle nesting on hunting behavior and movements of jaguars in the dry forest of northwest Costa Rica

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Abstract

Jaguars (*Panthera onca*) are opportunistic predators that prey on large profitable prey items, such as sea turtles at nesting beaches. Here, we use jaguar and sea turtle track-count surveys, combined with satellite telemetry of one jaguar, to evaluate whether jaguar hunting behavior and movements are influenced by seasonal sea turtle nesting in the Sector Santa Rosa of Área de Conservación Guanacaste in northwest Costa Rica. We used generalized linear models to evaluate the effect of moon phase and sea surface temperature on olive ridley (*Lepidochelis olivacea*) and green turtle (*Chelonia mydas*) nesting abundance, as well as the combination of these predictors on the frequency of jaguar predation activity (proximity to nesting beaches) and movements. For home-range size and location analyses, we calculated kernel density estimates for each season at three different temporal scales. Sea turtle nesting season influenced jaguar activity patterns, as well as sea turtle abundance was related to jaguar locations and predation events, but jaguar home-range size (88.8 km^2 overall) did not differ between nesting seasons or among temporal scales. Environmental conditions influenced sea turtle nesting and, as a consequence, also influenced jaguar movements and foraging activity. Our study defined the home range of a female jaguar in the tropical dry forest and its relationship to seasonally abundant turtles. Additional information related to the effect of tourism on jaguar–sea turtle interactions would improve conservation of these species at unique nesting beaches in the area.

KEYWORDS

Chelonia, Guanacaste, home range, *Lepidochelis*, moon phase, *Panthera*, seasonal ecosystem, telemetry

1 | INTRODUCTION

Highly seasonal ecosystems present a combination of challenges for wildlife that lead to physiological and behavioral adaptations (Astete et al., 2017; Blaum, Rossmanith, Schwager, & Jeltsch, 2007; Stoner & Timm, 2011). For example, jaguars (*Panthera onca*), which are widely distributed from northern Mexico to northern Argentina (UICN, 2019), exhibit seasonal movement patterns related to peaks of prey availability and abiotic factors (Carrillo, Fuller, & Saenz, 2009; Cavalcanti, 2008; Guilder, Barca, Arroyo-Arce,

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Gramajo, & Salom-Pérez, 2015). In the Pantanal of Brazil during the dry season, jaguars spend more time foraging near caiman (*Caiman crocodilus*) habitats (Cavalcanti, 2008), whereas in Corcovado, Costa Rica jaguars switch activity patterns related to spatiotemporal distribution of white-lipped peccaries (*Tayassu pecari*) and sea turtles (*Lepidochelys olivacea*, *Chelonia mydas*) (Carrillo, 2000).

Jaguars, however, are opportunistic predators preying on as many as 85 species, including most available animals weighing > 1kg (Carrillo, 2000; Rabinowitz & Nottingham, 1986); thus, efforts to understand the relationship of abiotic factors (seasonality and moon phases) and prey on jaguar spatial dynamics are area-specific. By using Global Positioning Satellite (GPS) telemetry, researchers can determine correlations between animals and their habitats, and thus record patterns of space use that likely influence their persistence (Gonzales- Borrajo, Lopez-Bao, & Palomares, 2017; Morellett et al., 2013). Not surprisingly, previous research emphasizing on jaguar spatial dynamics (e.g., Carrillo, 2000; Cavalcanti, 2008; De la Torre, Núñez, & Medellín, 2017; Gese, Terletzky, Cavalcanti, & Neale, 2018; Morato et al., 2018; Rabinowitz & Nottingham, 1986) has shown that seasonality influences area-specific movements of jaguars.

Sector Santa Rosa (SSR) in the dry forests of northwestern Costa Rica is likely home to one of the largest recovering jaguar populations in Costa Rica (Montalvo, Saenz, Ramirez, & Carrillo, 2015). It also contains two important sea turtle (olive ridley [*L. olivacea*] and green turtles [*C. mydas*]) nesting beaches, one characterized by a rare, seasonal sea turtle nesting aggregation (*arribada*; Playa Nancite), and the other (Playa Naranjo) characterized by year-round but seasonal solitary nesting (Behm, Hagerty, Drake, & Spotila, 2000; Cornelius, 1976; Cornelius & Robinson, 1982; Hughes & Richard, 1974; Valverde, Cornelius, & Claudettte, 1998). Here in particular, we hypothesize that during sea turtle nesting peaks, seasonal prey availability directly influences jaguar hunting behavior by increasing foraging activity near beaches and predation rates on sea turtles. In this study, we sought to identify the effect of seasonality and moon phases on jaguar foraging distances to sea turtle nesting beaches; seasonal spatiotemporal patterns on jaguar home-range size, and frequency of jaguar's sea turtle predation events related to season, sea turtle abundance, and moon phases.

2 | Methods

2.1 | Study area

This study was conducted in SSR, within one of the three national parks of Área de Conservación Guanacaste (ACG) located in northwest Costa Rica (10°53′01″N 85°46′30″W; Boza, 1992). SSR encompasses 387 km^2 and is dominated by the few remaining tropical dry forests in Central America (Gillespie, Grijalva, & Farris, 2000; Janzen, 1988), with average annual rainfall of 1,600 mm that is highly seasonal (monthly averages from 0 mm to 1,040 mm); the wet season (months with ≥ 40mm of rain) is May to November, and the dry season (with almost no rain and temperatures over 37°C) is December to April. Due the rarity of dry forest ecosystems, a large-scale restoration effort was initiated in the 1980s involving protected area status, the recovery of abandoned pastures by active fire suppression (Klemens, Deacon, & Cavender-Bares, 2011), and protection from many human activities of the Park's two important sea turtle nesting beaches. At Playa Nancite (length = 1.05 km), where thousands of turtles come ashore during the wet months (Fonseca, Murillo, Guadamuz, Spínola, & Valverde, 2009; Valverde et al., 1998), only researchers are allowed visit during the arribada. At Playa Naranjo (length = 5.64 km), there is a staffed ranger station and campground where up to 40 tourists may stay and use the beach year-round, even though there is an increasing pattern of seasonal turtle nesting (Drake et al., 2003). There is a significant ridge that separates the beaches, and an estuary that cuts through the northern part of Playa Naranjo, but neither of these is likely a barrier to jaguar movements.

2.2 | Data collection

We gathered previous sea turtle nesting data surveys from peer-reviewed and technical papers for both Playa Nancite (1980–2011) and Playa Naranjo (2013–2015). When the raw data from turtle nesting surveys was not available, we used the R package "digitalize" to retrieve data from old figures (Poisot, 2011). Opportunistic sea turtle track-count surveys also were conducted at Playa Naranjo during 2013–2015. Each morning, we walked along Playa Naranjo at 2 km/hour and registered activity from the previous night; sea turtle track-counts by species, jaguar presence (i.e., jaguar tracks on the beach), and jaguar predation events (i.e., jaguar-killed turtles). Additional information such moon phase (Lazaridis, 2014) was gathered for analysis.

We also monitored the movements of a single three-year-old jaguar female fitted with a GPS collar (Lotek Engineering; http://www.lotek.com) programmed to record the jaguar's position every 2 hr, and activity every 5 min, during 577 days (12/1/2014–6/30/2016). The jaguar was captured using a foot snare (Frank, Simpson, & Woodroffe, 2003), and chemically immobilized using a dart projectile (Dan-inject; https://www.dan-inject.com) with a combination of 5 mg/kg of ketamine (10% ketamine; Bremer Pharma GmbH) mixed with 2mg/kg xylazine (Procin Equus 10%, Pisa Agropecuaria) (Deem, & Keresh, 2001). Handling and capture protocols followed guidelines of the American Society of Mammalogists (Silkes & Gannon, 2011) and also were approved by the Environmental Minister of Costa Rica (ACG-PI-034–2014), following the ethics and research procedure guidelines of the National University.

2.3 | Statistical analysis

To fulfill the model assumptions, we followed the data exploration protocol designed by Zuur, Ieno, and Elphick (2010), by using the statistical software R version 3.1.3 (R Core Team, 2015) to perform data analysis. For the turtle count data (Tur) and the distance data from

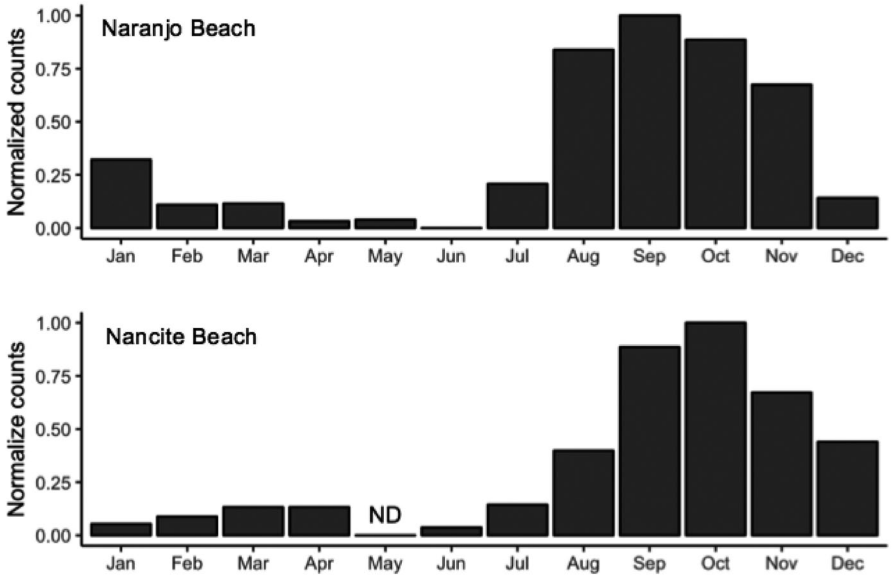

FIGURE 1 Monthly mean-normalized counts of sea turtles (olive ridley *Lepidochelis olivacea*, and green turtle *Chelonia mydas*) at Naranjo Beach (2013–2015) and Nancite Beach (1980–2011) in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica. Actual average peak counts were 212 nesting turtles at Naranjo in September versus 2,197 at Nancite in October

each jaguar location to the nesting beaches (Dist. beach), we used generalized lineal models (GLM—) with a log link function (Venables & Ripley, 2002), assuming negative binomial error distribution due to overdispersion issues, and a binomial distribution for the jaguar predation data (Pred. events) (Forte, 2015). In order to assess the effect of turtle nesting abundance season (seas) and moon phases (moon) on the jaguar's distances from nesting beaches and the frequency of jaguar predation events, our models include these variables as predictors (moon, seas).

Daily activity patterns were estimated from the collar's motion sensor, and aggregated seasonally by hour, using a Welch *t* test to compare seasonal differences. For home-range analysis, we calculate the KDE (kernel density estimate) using both 50% and 95% isopleth contours with the R package "rhr" (Signer & Balkenhol, 2015), using season (peak versus. off season) at three different temporal scales (month, week, and season) as covariates. Additionally, side fidelity tests also were used to determine whether the animal showed patterns associated with specific areas within SSR by contrasting the mean squared distance (MSD) and a linearity index (LI) from the center of activity with a permuted distribution (i.e., if the mean observed value for the MSD and LI are below the permuted threshold one can conclude there is site fidelity) following Signer and Balkenhol (2015) method..

TABLE 1 Models describing the effect of turtle nesting season (seas) and moon phases (moon) on distances of a GPS-collared jaguar to the closest nesting beach (Dist. beach) in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

Model	*df*	AIC	Δ AIC	ω
Dist. beach = seas ×moon	9	106,419	0	1
Dist. beach = seas +moon	6	106,435	16	<0.001
Dist. beach = seas	3	106,450	31	<0.001
Dist. beach = Moon	5	106,789	369	<0.001
Dist. beach = intercept	2	106,809	389	<0.001

3 | RESULTS

Mean-normalized peak counts of sea turtles (species combined) at both beaches depicted the same seasonal nesting trend (peak from July to January; Figure 1) throughout the year, with maximum mean sea turtle counts at Playa Naranjo of ~ 212 in September versus

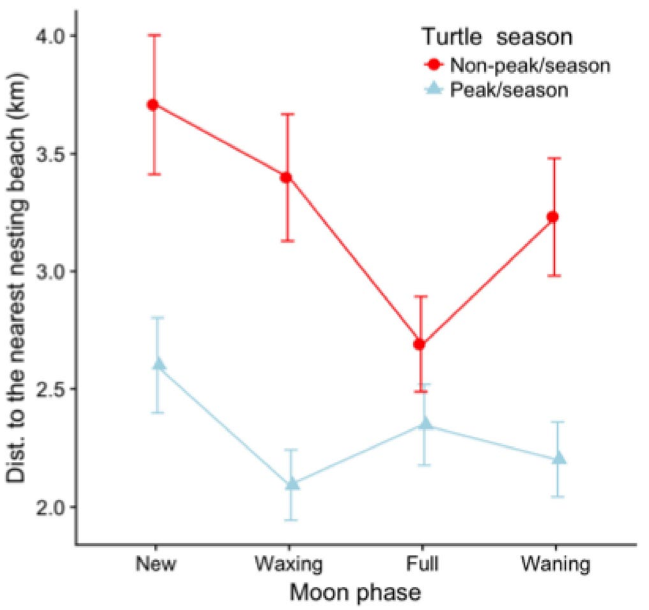

FIGURE 2 Mean GPS-collared jaguar distances (km) to the nearest turtle nesting beach [mean ± 95% confidence interval] as influenced by moon phase and turtle nesting abundance season in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

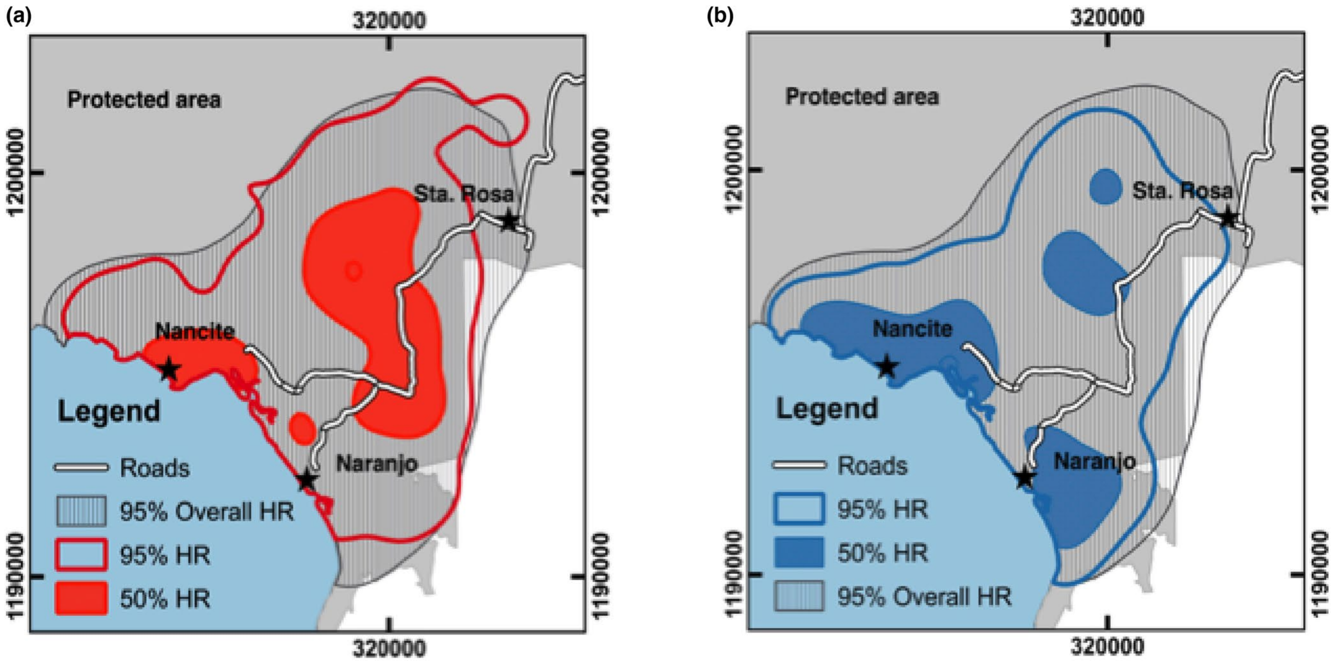

FIGURE 3 Seasonal home-range sizes (km) of a GPS-collared female jaguar during the non-peak (A) and peak season of sea turtle nesting (B) at Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

~2,197 at Playa Nancite in October, and strong evidence of sea turtle nesting seasonality.

We also collected 5,924 GPS locations of the collared jaguar during December 2014–June 2016. GLM modeling testing for seas and moon effects on jaguar distances to the closest nesting beach produced a top model with the interaction of moon and seas (Table 1; AIC ω = 1) markedly influencing jaguar location distances to nesting beaches. As expected, the collared jaguar was farther (~1.06 km) from nesting beaches during non-peak nesting season (Figure 2). With regard to moon phase, during peak nesting season, the collared jaguar stayed closer to nesting beaches on waxing and waning moon phases, whereas during the non-peak season the closest mean distances registered for this jaguar were on full and waning moon phases (Figure 2).

The overall home range (95% HR) size of the collared jaguar was 88.8 km^2, and the HR estimates for the non-peak (50% HR: 17.6 km^2, 95% HR: 72.3 km^2) and peak nesting seasons (50% HR: 18.1 km^2, 95% HR: 68.2 km^2) were similar, though the spatial distribution of the 50% HRs varied (Figure 3). We observe more spatial aggregation at Naranjo and Nancite Beaches during the nesting peak season (Figure 3), whereas during the non-peak nesting season 50% HR was concentrated in the middle of SRNP and a small section of Nancite Beach (Figure 3). Further analysis of site fidelity indicated that the mean square distance from the center of activity (6.8 km; CI 95%: 4.01–9.08), as well as the linearity index (0.050; CI 95%: 0.015–1.55), did not show statistical evidence of site fidelity. With regard to spatiotemporal variation of the GPS-collared jaguar's HR sizes, we did not find statistical evidence of variation between monthly (t = 0.20, df = 14.83, p = .84) and weekly (t = 0.8, df = 50, p = .4) HR sizes (Figure 4), but during the

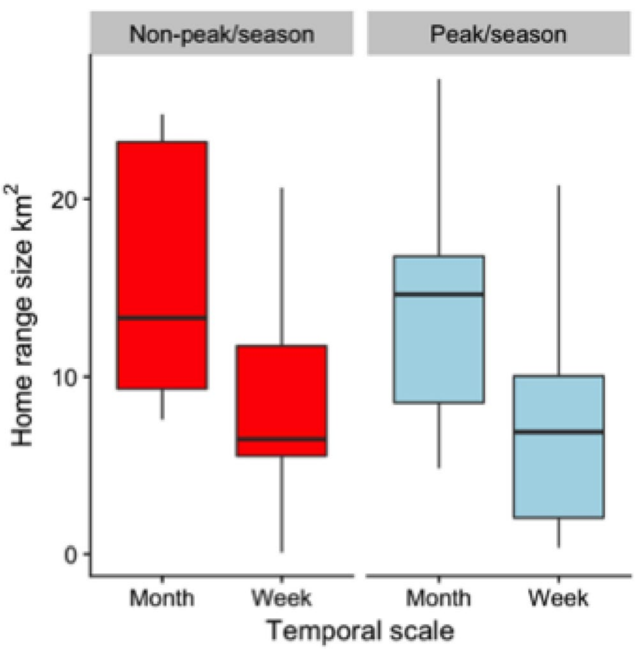

FIGURE 4 Spatiotemporal variation of a GPS-collared jaguar's monthly and weekly home-range sizes (km^2) between seasons of differing turtle nesting abundance at Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

non-peak nesting season the HRs were larger (Figure 4). The jaguar activity patterns for both non-peak and peak nesting seasons followed similar trends, being more active from 0:00 to 11:00–12:00 and gradually start decreasing until the lowest activity peak at 18:00, followed by a gradual increase until 0:00 (Figure 5). The

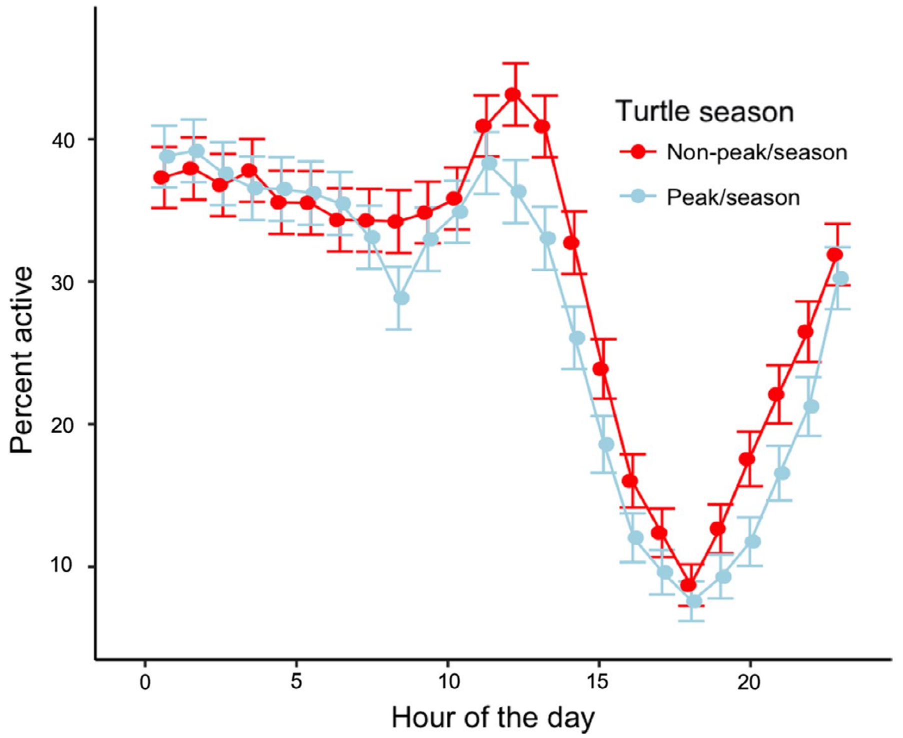

FIGURE 5 Activity patterns of a GPS monitored female during the non-peak and peak season of sea turtle nesting in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica (The number of automatic activity records per hour was 12)

overall pattern showed this jaguar was active the most at night, decreasing its activity during the day. Activity patterns comparison showed statistical differences between non-peak and peak nesting seasons (t = 3.6582, df = 18,942, p = .0002), suggesting this jaguar slightly increased activity during day hours on non-peak nesting season (Figure 5).

The GLM modeling of the occurrence of predation events at Playa Naranjo showed turtle abundance as the top model (Table 2; AIC ω = 0.6), as well as the interaction of peak nesting season (Table 2; AIC ω = 0.39). Jaguar predation hot spots at both beaches showed a specific pattern of aggregation at Playa Naranjo with most of the sea turtle carcasses at the southern section (Figure 6), whereas predation hot spots at Playa Nancite were evenly distributed, with the highest carcass concentrations at both north and southern sections (Figure 6). GPS locations of the collared jaguar matched the pattern of predation hot spots determined from carcasses (Figure 6), suggesting high concentration of jaguar locations near the estuary at Playa Naranjo where, due to difficult accessibility on this beach section, we could not sample turtle carcasses; nevertheless we speculate the same pattern previously observed across both beaches.

TABLE 2 Models describing the effect of sea turtle abundance (tur), turtle nesting season (seas) and moon phase (moon) on jaguar predation events (Pred. Events; i.e., jaguar-killed turtles) at Playa Naranjo in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

Model	*df*	AIC	Δ AIC	ω
Pred. events = tur	2	228	0	0.60
Pred. events = tur × Seas	4	229	1	0.39
Pred. events = tur × moon	1	237	9	0.007
Pred. events = tur × moon + seas	8	239	11	0.002
Pred. events = intercept	1	137	16	0.001

4 | DISCUSSION

We used track-count surveys of sea turtles and GPS telemetry of a female jaguar to evaluate the influence of turtle nesting season on jaguar hunting behavior assessing home-range size, activity patterns, and predation patterns on sea turtles. Our results indicated a seasonal increase in sea turtle availability (Behm et al., 2000; Cornelius & Robinson, 1982; Fonseca et al., 2009; Valverde et al., 1998) that shaped ecological interactions. Moon phase, sea surface temperature, and the time of the year influence the number of sea turtles that come ashore, perhaps due to sea surface temperature affecting the internal physiology of sea turtle, as well as constraining sea grass nutrition quality in need to prepare clutches to laying (Hamann, Limus, & Owens, 2003; Houtan, Halley, & Marks, 2015). Additionally, observations by us and others (Carrillo et al., 2009; Herrera, 2016; Houtan et al., 2015) indicate sea turtles likely choose specific moon phases to nest, perhaps due to the amount of energy intake and time spent to come ashore and nest, as well as because the moon brightness might make sea turtles more vulnerable to predators.

Jaguar location distances from nesting beaches were frequently closer on the peak nesting season, interacting with moon phases, similar to the finding of previous studies (e.g., Carrillo, 2000; Carrillo et al., 2009); this suggests a seasonal foraging strategy by jaguars to maximize their energy budget. Jaguars may also synchronize births

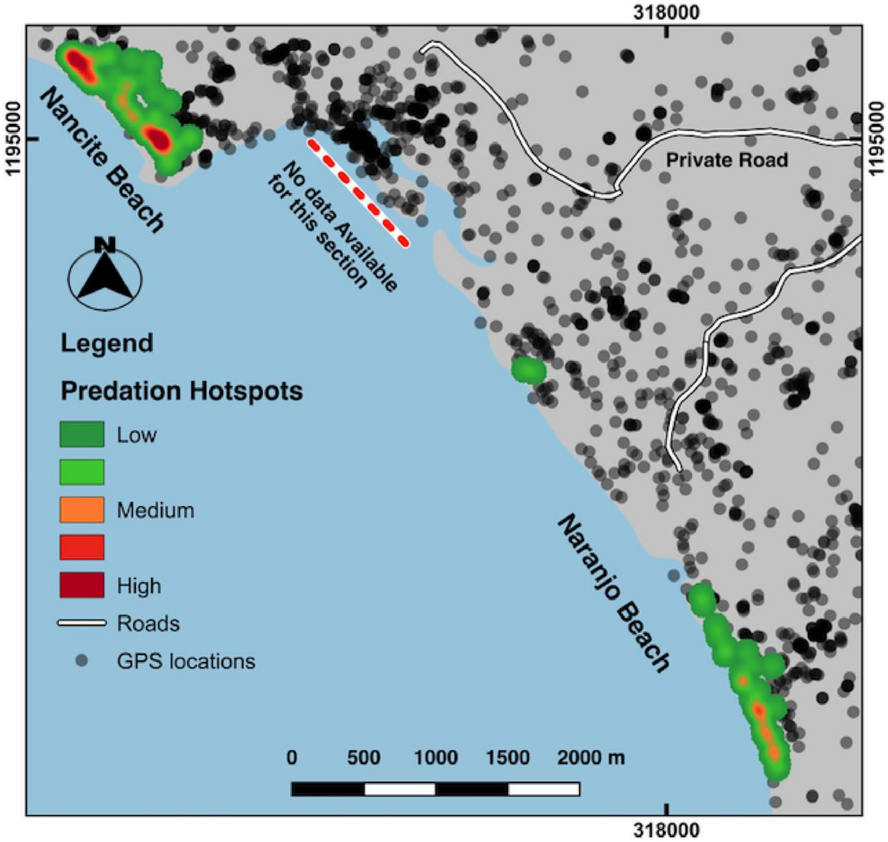

FIGURE 6 Locations of jaguar-predated turtle carcasses ("Predation hot spots"; cf. Escobar-Lasso et al., 2017) and a GPS-collared jaguar at Nancite and Naranjo beaches in Sector Santa Rosa of Area de Conservación Guanacaste in northwestern Costa Rica

with peaks of sea turtle abundance as a strategy to increase offspring survival and recover body mass after birthing (Bergstrom, Thompson, Melin, & Fedigan, 2017; Campos et al., 2017); we have recorded frequent field sightings of females with offspring at nesting beaches during peak nesting (unpublished information).

Early telemetry studies described seasonal responses on jaguar home-range sizes owing to prey abundance peaks on time (Astete et al., 2017; Carrillo, 2000; Cavalcanti, 2008; Gese et al., 2018). Though we found no statistical evidence of seasonal changes in home-range sizes, seasonal core areas changed location from one season to another, concentrating mostly on nesting beaches during sea turtle peak season and matching with locations of predated sea turtle carcasses (Alfaro et al., 2016; Escobar-Lasso et al., 2017). Changes in prey distribution over time and though space has consequences for predators, because if prey respond to environmental changes, predators follow the same trend (Sunquist & Sunquist, 2002). For example, in the Kalahari Desert when large prey are dispersed, the home-range size of a lion (*Panthera leo*) pride increases 5 times the regular home-range size (Sunquist & Sunquist, 1989). The home-range size estimated in this study for a female jaguar was larger (88.8 km^2) than that reported by Carrillo (2000; 20.5 km^2), the only other one in Costa Rica. Even though multiple studies have elsewhere estimated varying female jaguar home-range sizes (15.3–722.5 5 km^2), there is still little knowledge concerning the relationship of home-range size with prey availability (McBride & Thompson, 2017; Morato et al., 2018). Thus, the enormous seasonal turtle availability and the number of solitary nesting beaches across the Área de Conservación Guanacaste make this area unique, and likely allow for the long-term persistence of jaguars and other potential predators that opportunistically use this marine resource. Elsewhere, analysis of jaguar predation events upon sea turtles showed a strong positive relationship between turtle abundance and the frequency predation events (Guilder et al., 2015). Jaguar activity patterns also showed how this individual was less active during peak nesting season, suggesting synchronic prey availability patterns may lead predator aggregation and coordinated movements as behavioral response in places where prey are seasonally abundant (Penteriani, Fortuna, Melián, Otalora, & Ferrer, 2006). Therefore, jaguars may save energy by aggregating themselves in places such Playa Naranjo and Playa Nancite where easy-to-capture sea turtles also are concentrated in high densities.

In addition to jaguar behavioral responses due to seasonal marine prey availability in this study, is worthwhile to mention the important role of jaguars as a top predator (Estes et al., 2011), linking marine biomass with terrestrial ecosystems. Jaguar are known for their biting strength (Moral-Sachetti, Lameda-Camacaro, Vázquez, & Zenteno Cárdenas, 2011), thus enabling the use of a variety of potential prey not available to other carnivores (Weckel, Giuliano, & Silver, 2006). Therefore, sea turtle predation by jaguars, by moving marine biomass to terrestrial ecosystems, may benefit multiple scavenger organisms that could take the advantage of sea turtle remains acting as a top-down cascade effect in this unique place.

In summary, our results provide strong evidence of jaguar behavioral responses linked to peaks of seasonal availability of sea turtles in the dry forest ecosystem. Climate and environment conditions directly influenced biology of sea turtle nesting and, as a consequence, also constrains jaguar movements and foraging activity. Optimal foraging theory predicts that predators seek out prey in terms of energy (MacArthur & Pianka, 1966), and our study partially fulfilled this prediction. Even though our study only used GPS telemetry data from one individual, our results were consistent with the sea turtle track and carcass count surveys and previous data. Finally, knowledge of jaguar home-range sizes and their variation with prey in seasonal ecosystems might contribute to improved conservation, especially in places such Playa Naranjo with the dual values of conservation of endangered species and tourism; our study defines a baseline home-range size for jaguars in the tropical dry forest, and focuses the importance of seasonal sea turtle availability in influencing the terrestrial dynamics of large predators and making this resource accessible for other organisms.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2bvq83bmr (Montalvo et al., 2020).

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REFERENCES

Alfaro, L., Montalvo, V., Guimarães, F., Saenz, C., Cruz, J., Morazan, F., & Carrillo, E. (2016). Characterization of attack events on sea turtles (*Chelonia midas* and *Lepidochelys olivacea*) by Jaguar (*Panthera onca*) in Naranjo Sector, Santa Rosa National Park, Costa Rica. *International Journal of Conservation Science*, *7*, 101–108.

Astete, S., Marinho-Filho, J., Machado, R. B., Zimbres, A. T., Jácomo, R., Sollmann, N., … Silveira, L. (2017). Living in extreme environments: Modeling habitat suitability for jaguars, pumas, and their prey in a semiarid habitat. *Journal of Mammalogy*, *98*, 464–474.

Behm, E., Hagerty, M., Drake, D., & Spotila, J. (2000). Marine turtle nesting activity on Playa Naranjo, Santa Rosa National Park, Costa Rica 1998–99. 20th Annual Sea Turtle Symposium. 232–234.

Bergstrom, M., Thompson, M., Melin, A., & Fedigan, L. (2017). Using urinary parameters to estimate seasonal variation in the physical condition of female white-faced capuchin monkeys (*Cebus capucinus imitator*). *American Journal of Physiology Anthopology*, *163*, 707–715.

Blaum, N., Rossmanith, E., Schwager, M., & Jeltsch, F. (2007). Responses of mammalian carnivores to land use in arid savanna rangelands. *Basic Applied Ecology*, *8*, 552–564. https://doi.org/10.1016/j.baae.2006.09.003

Boza, M. (1992). *National parks of Costa Rica, incafo*, 2nd ed. Illinois, USA: Northwestern University Press.

Campos, F., Alberts, C., Altmann, J., Brockman, D. K., Cords, M., Morris, W. F., … Fedigan, L. M. (2017). Does climate influence the demography of wild primates? Evidence from long-term life-history data in seven species. *Global Change Biology*, *23*, 4907–4921.

Carrillo, E. (2000). *Ecology and conservation of white-lipped peccaries and jaguars in Corcovado National Park*. PhD Dissertation. University of Massachusetts, Massachusetts Amherst.

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

Cavancanti, S. M. C. (2008). *Predator-prey relationship and spatial ecology of jaguars in the southern Pantanal, Brazil: implications for conservation and management*. PhD Dissertation. Utah State University, Logan, UT.

Cornelius, S. E. (1976). Marine turtle nesting activity at Playa Naranjo, Costa Rica. *Brenesia*, *8*, 1–27.

Cornelius, S. E., & Robinson, C. (1982). *Abundance, distribution and movements of olive ridley sea Turtles in Costa Rica, II*. Final Report On U.S Fish and Wildlife Service Endangered Species.

De La Torre, J. A., Núñez, J. M., & Medellín, R. (2017). Spatial requirements of jaguars and pumas in Southern Mexico. *Mammal Biology*, *84*, 52–60. https://doi.org/10.1016/j.mambio.2017.01.006

Deem, L., & Karesh, W. (2001). *The jaguar health program manual. Field veterinary program*. New York, NY: Wildlife Conservation Society. Retrieved from http://www.panthera.org/node/415. Accessed 8 March 2015.

Drake, D. L., Behm, J. E., Hagerty, M. A., Mayor, P. A., Goldenberg, S. J., & Spotila, J. R. (2003). Marine turtle nesting activity at Playa Naranjo, Santa Rosa National Park, Costa Rica, for the 1998–1999 season. *Chelonian Conservation and Biology*, *4*, 675–678.

Escobar-Lasso, S., Gil-Fernández, M., Sáenz, J., Carrillo, E., Wong, G., Fonseca, L., & Gómez-Hoyos, D. (2017). Distribution and hotspots of the feeding areas of jaguars on sea turtles at a national park in Costa Rica. *Neotropical Biology and Conservation*, *12*, 2–11. https://doi.org/10.4013/nbc.2017.121.01

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., … Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*, 301–306. https://doi.org/10.1126/science.1205106

Fonseca, L., Murillo, G., Guadamuz, L., Spínola, M., & Valverde, R. (2009). Downward but stable trend in the abundance of arribada Olive Ridley Sea Turtles (*Lepidochelys olivacea*) at Nancite Beach, Costa Rica (1971–2007). *Chelonian Conservation Biology*, *8*, 19–27.

Forte, R. (2015). *Mastering predictive analytics with R*. Birmingham, UK: Packt Publishing Ltd.

Frank, L., Simpson, D., & Woodroffe, R. (2003). Foot snares: An effective method for capturing African lions. *Wildlife Society Bulletin*, *31*, 309–314.

Gese, E. M., Terletzky, P. A., Cavalcanti, S., & Neale, C. M. U. (2018). Influence of behavioral state, sex, and season on resource selection by jaguars (*Panthera onca*): Always on the prowl? *Ecosphere*, *9*, 1–16.

Gillespie, T. W., Grijalva, A., & Farris, C. N. (2000). Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology*, *147*, 37–47.

Gonzales- Borrajo, N., Lopez-Bao, J. V., & Palomares, F. (2017). Spatial ecology of jaguars, pumas, and ocelots: A review of the state of knowledge. *Mammal Review*, *47*, 62–75.

Guilder, J., Barca, B., Arroyo-Arce, S., Gramajo, R., & Salom-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*, 65–72. https://doi.org/10.1016/j.mambio.2014.11.005

Hamann, M., Limus, C., & Owens, D. (2003). Reproductive cycles of males and females. In P. Lutz, J. Musick & J. Wyneken (Eds.), *The biology of sea turtles*, Vol. *II* (pp. 135–163). Boca Raton, Florida: CRC Press.

Herrera, H. (2016). Actividad diaria y depredación de tortugas marinas por el jaguar (Panthera onca) en el Parque Nacional Santa Rosa, Costa Rica. MSc Dissertation. Instituto Internacional en Conservación y Manejo de Vida Silvestre, Universidad Nacional, Heredia, Costa Rica.

Houtan, K., Halley, J. M., & Marks, W. (2015). Terrestrial basking sea turtles are responding to spatio-temporal sea surface temperature patterns. *Biology Letters*, *11*, 20140744. https://doi.org/10.1098/rsbl.2014.0744

Hughes, D., & Richard, J. D. (1974). The nesting of the Pacific Ridley Turtle *Lepidochelys olivacea* on Playa Nancite, Costa Rica. *Marine Biology*, *24*, 97–107. https://doi.org/10.1007/BF00389343

IUCN (2019). *International union for conservation of nature*, *Red list of threatened species*. Gland, Switzerland: IUCN. Retrieved from http://www.redlist.org. Accessed 18 January 2019.

Janzen, D. H. (1988). Guanacaste National Park: Tropical ecological and biocultural restoration. In J. Cairns (Ed.), *Rehabilitating damaged ecosystems*, Vol. *11* (pp. 143–192). London, UK: CRC Press.

Klemens, J. A., Deacon, N. J., & Cavender-Bares, J. (2011). Pasture recolonization by a tropical oak and the regeneration ecology of seasonally dry forests. In R. Dirzo, H. S. Young, H. A. Mooney & G. Ceballos (Eds.), *Seasonally dry tropical forests* (pp. 221–237). Washington, DC: Island Press.

Lazarridis, E. (2014). *Lunar: Lunar phase & distance, seasons and other environmental factors (Version 0.1-04)*. Retrieved from http://statistics.lazaridis.eu. Accessed 18 March 2019.

MacArthur, R., & Pianka, E. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*(916), 603–609. https://doi.org/10.1086/282454

MacBride, R., & Thompson, J. (2017). Space use and movement of jaguar (panther onca) in western Paraguay. *Mammalia*, *82*(6), 540–549.

Montalvo, V., Fuller, T. K., Saénz-Bolaños, C., Cruz, J. C., Hagnauer, I., Herrera, H., & Carrillo, E. (2020). Data from: Influence of sea turtle nesting on hunting behavior and movements of jaguars in the dry forest of northwest Costa Rica. Dryad Digital Repository.https://doi.org/10.5061/dryad.2bvq83bmr

Montalvo, V., Saenz, C., Ramirez, S., & Carrillo, E. (2015). Monitoreo de la abundancia del jaguar *(Panthera onca*) otros felinos y sus presas potenciales en el Parque Nacional Santa. Rosa, Costa Rica. *Cuadernos De Investigación UNED*, *7*, 305–311.

Moral-Sachetti, J., Lameda-Camacaro, F., Vázquez, J., & Zenteno Cárdenas, R. (2011). Fuerza de mordedura y estrés mandibular en el jaguar (*Panthera onca)* durante la depredación de pecaríes (Artiodactyla: Tayassuidae) mediante la fractura de sus cráneos. *Acta Zoológica Mexicana*, *27*(3), 757–776. https://doi.org/10.21829/azm.2011.273779

Morato, R., Connette, J. A., Stabach, R., De-Paula, R., Ferraz, K., Kantek, D., … Leimguber, P. (2018). Resource selection in an apex predator and variation in response to local landscape characteristics. *Biology Conservation*, *228*, 233–240. https://doi.org/10.1016/j.biocon.2018.10.022

Morellett, N., Bonenfant, C., Börger, L. F., Ossi, F., Cagnacci, M., Heurich, P., … Mysterud, A. (2013). Seasonality, weather and climate effect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, *82*, 1326–1339.

Penteriani, V., A. Fortuna, M., J. Melián, C., Otalora, F., & Ferrer, M. (2006). Can prey behaviour induce spatially synchronic aggregation of solitary predators? *Oikos*, *113*, 497–505. https://doi.org/10.1111/j.0030-1299.2006.14547.x

Poisot, T. (2011). The digitize package: Extracting numerical data from scatterplots. *The R Journal*, *3*, 25–26. https://doi.org/10.32614/RJ-2011-004

R Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/. Accessed 15 April 2019.

Rabinowitz, A., & Nottingham, B. (1986). Ecology and behavior of the jaguar (*Panthera onca*) in Belize, Central America. *The Zoological Society of London*, *210*, 149–159.

Signer, J., & Balkenhol, N. (2015). Reproducible home ranges (rhr): A new, user-friendly R package for analyses of wildlife telemetry data. *Wildlife Society Bulletin*, *39*, 358–363.

Silkes, R. S., Gannon, W. & Animal Care And Use Committee Of The American Society Of Mammologists (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy.*, *92*, 235–253. https://doi.org/10.1644/10-MAMM-F-355.1

Stoner, K., & Timm, R. (2011). Seasonally dry tropical forest mammals: Adaptation and seasonal patterns. In R. Dirzo, H. Young,H. Mooney & G. Ceballos (Eds.), *Seasonally dry tropical forest mammals: Adaptation and seasonal patterns* (pp. 85–106). Washington, DC: Island Press.

Sunquist, M., & Sunquist, F. (1989). Ecological constraints on predation by large felids. In J. Gittleman (Ed.), *Carnivore behavior, ecology and evolution* (pp. 283–301). New York, NY: Cornell University Press.

Sunquist, M., & Sunquist, F. (2002). *Wild cats of the world*. Chicago, IL: University of Chicago Press.

Valverde, R., Cornelius, S., & Claudettte, M. (1998). Decline of the olive ridley sea turtle (*Lepidochelys olivacea*) nesting assemblage at Nancite Beach, Santa Rosa National Park, Costa Rica. *Chelonian Conservation Biology*, *3*, 58–63.

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*, 4th ed. New York, NY: Springer Science & Business Media.

Weckel, M., Giuliano, W., & Silver, S. (2006). Jaguar (*Panthera onca*) feeding ecology: Distribution of predator and prey through time and space. *Journal of Zoology*, *270*, 25–30. https://doi.org/10.1111/j.1469-7998.2006.00106.x

Zuur, A. F., Ieno, E. N., & Elphick, C. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

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