Received: 7 August 2025 | Revised: 26 November 2025 | Accepted: 29 December 2025

DOI: 10.1002/jwmg.70174

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

RESEARCH ARTICLE

Indirect effects of fast-growing urban development on wildlife in a coastal protected area of Costa Rica

Keilor E. Cordero-Umaña[1,2] | **Kortney Stevens[2]** | **Adam Yaney-Keller[3]** | **Javier López Navas[2]** | **Frank V. Paladino[2,4]** | **James R. Spotila[2,5]** | **Pilar Santidrián Tomillo[6]**

[1]Menéndez Pelayo International University (UIMP), Doctoral Program in Science and Technology UIMP-CSIC, C. Isaac Peral 23, Madrid 28040, Spain

[2]The Leatherback Trust, Goldring-Gund Marine Biology Station, Playa Grande, Santa Cruz 50308, Costa Rica

[3]Monash University, Wellington Rd, Clayton, Victoria 3800, Australia

[4]Department of Biology, Purdue University, Fort Wayne, IN 46805, USA

[5]Department of Biodiversity, Earth and Environmental Science, Drexel University, Philadelphia, PA 19104, USA

[6]Moll de Ponent s/n, Centre Oceanogràfic de Illes Balears, Instituto Español de Oceanografía (COB-IEO), CSIC, Palma de Mallorca 07015, Spain

Correspondence

Keilor E. Cordero-Umaña, Menéndez Pelayo International University (UIMP), Doctoral Program in Science and Technology UIMP-CSIC, C. Isaac Peral 23, 28040, Madrid, Spain.
Email: ke.cordero@posgrado.uimp.es and kecordero95@gmail.com

Pilar Santidrián Tomillo, Centre Oceanogràfic de Illes Balears, Instituto Español de

Abstract

Urban development facilitates predictable anthropogenic food subsidies (PAFS), allowing opportunistic species to thrive. Access to PAFS can drive population increases in certain species, producing cascading effects that may directly or indirectly affect others, including species already in decline or of conservation concern. We studied the effect of PAFS in a Protected Area in Costa Rica, Parque Nacional Marino Las Baulas (PNMB), which was established to protect sea turtles. We quantified urban growth since the Park was established, assessed the effects of PAFS in trash containers on the presence and activity of wildlife species, and evaluated the increase in sea turtle nest predation over time. Since the Park was established (1991), there has been a > 10-fold increase in the number of buildings in the area, mainly within its buffer zone. We identified 8 native species extracting food from garbage containers at PNMB, with northern raccoons (*Procyon lotor*) comprising most detections (84%), and 4 other species that are potential predators of sea turtle eggs. The number of detections and access to garbage containers was influenced by location and type of container. Areas with more development had more wildlife detections around garbage containers. Additionally, the

Oceanografía (COB-IEO), CSIC, Moll de Ponent s/n, 07015 Palma de Mallorca, Spain.
Email: mpilar.santidrian@ieo.csic.es

Funding information
National Fish and Wildlife Foundation, Grant/Award Number: 82052

percentages of sea turtle clutches predated and clutches that were relocated to avoid predation increased since predation was first monitored in the 2011–2012 nesting season. We hypothesized that urban development promoted PAFS at PNMB, possibly increasing the number of raccoons, which in turn, increased predation of sea turtle nests. Although further research is needed to confirm this link, limiting urban development and improving waste management are essential to protect sea turtle nests at PNMB.

KEYWORDS
Costa Rica, food subsidies, garbage management, nest predation, PAFS, Parque Nacional Marino Las Baulas, *Procyon lotor*, sea turtles, urban growth

Since the 1950s, urban development has increased exponentially worldwide (United Nations 2018), often replacing natural environments (Hamer and McDonnell 2010). Living in human-dominated landscapes can be challenging for some species, as they may need to obtain resources under elevated levels of anthropogenic disturbance (Ditchkoff et al. 2006, Lowry et al. 2013). Yet, while some populations may decline or disappear under human-related pressures, others adapt and even thrive, taking advantage of the increased availability of anthropogenic resources, such as food waste (Etter et al. 2002, Bateman et al. 2012, Graser et al. 2012).

Yearly, a third of the food produced for human consumption is lost or wasted worldwide, which represents losses of more than one billion tons (Food and Agriculture Organization of the United Nations 2011). Discarded food can become highly predictable in space and time, acting as a major attractant to wildlife, as it can be more abundant and easily accessible than natural food sources (Oro et al. 2013, Real et al. 2017). As a result, species able to exploit predictable anthropogenic food subsidies (PAFS) can benefit by improving their body condition, survival, or breeding success (Etter et al. 2002, Ditchkoff et al. 2006, Oro et al. 2013). The proliferation of species using PAFS can negatively impact other species through competition or predation (Carey et al. 2012, Oe et al. 2020). Such effects are particularly concerning when populations exploiting PAFS become overabundant and interact with species already in decline or of conservation concern, as even minor increases in predation or competition could have detrimental effects on their populations (Garrott et al. 1993, Carey et al. 2012).

Sea turtles nest on tropical and temperate beaches around the world and, because there is no parental care, their clutches are particularly vulnerable to predation (Leighton et al. 2011, Welicky et al. 2012). Nest predation is a natural source of mortality that provides energy and nutrient inputs to the biotic community of beach ecosystems (Madden et al. 2008). However, in areas where predators become overabundant, increases in predation of sea turtle nests can have an impact at the population level, by reducing offspring survival and population recruitment (Welicky et al. 2012, Heithaus 2013). For instance, at Hobe Sound National Wildlife Refuge in Florida, USA, northern raccoons (*Procyon lotor*; hereafter raccoons) and armadillos (*Dasypus novemcinctus*) predated up to 95% of loggerhead (*Caretta caretta*) nests in the 1990s, causing a loss of >60,000 hatchlings per season (Engeman et al. 2005). Likewise, in Qatar, Ruppell's foxes (*Vulpes rueppellii*) predated >80% of *in situ* hawkbill (*Eretmochelys imbricata*) nests in a year, greatly reducing reproductive success (Ficetola 2008). Similarly, high predation levels have been observed in Baja California (Mexico) and Naranjo Beach (Costa Rica), where 81% and 74% of olive ridley (*Lepidochelys olivacea*) nests, respectively, were predated by coyotes (*Canis latrans*) in a single season (Drake et al. 2003, Méndez-Rodríguez and Álvarez-Castañeda 2016).

On the North Pacific coast of Costa Rica, the area of Parque Nacional Marino Las Baulas (PNMB) has experienced accelerated urban development since its establishment in the 1990s (Honey 2003). This development has been driven by the growing demands of tourism, possibly due to the country's recognition as a green destination and well-established protected areas system (Vázquez Muñoz 2002, Instituto Costarricense de Turismo 2024). As a result, housing and tourist activities could generate a large amount of waste that could be accessible to wildlife, potentially benefiting opportunistic species. The number of raccoons may have subsequently increased at PNMB, which could have resulted in a rise in predation of olive ridley turtle clutches on the beach (Cornhill 2021).

Parque Nacional Marino las Baulas was established in 1991 to mainly protect leatherback turtles (*Dermochelys coriacea*), which are critically endangered in the Eastern Tropical Pacific (Wallace et al. 2013). In addition, the Park also hosts nesting olive ridley turtles (Dornfeld et al. 2015) and green turtles (*Chelonia mydas*), which have been classified as vulnerable and endangered, respectively, by the International Union for the Conservation of Nature (Seminoff 2004, Abreu-Grobois and Plotkin 2008). Because all sea turtle species that nest at PNMB have some level of endangerment, increasing nest predation could not only hinder the conservation goals of the Park but also contribute to further population declines. Thus, understanding the effects of urban growth on wildlife near or inside Protected Areas can help guide conservation actions to better protect them. We hypothesized that urban growth over the years resulted in an increase in PAFS that favored the proliferation of raccoons at PNMB, and this, in turn, increased nest predation and threatened sea turtles. To this end, we aimed to determine the level of urban growth since the establishment of the National Park, assess the effect of PAFS in trash containers on the presence and activity of wildlife species at PNMB, and evaluate the increase in sea turtle nest predation over time.

STUDY AREA

Parque Nacional Marino las Baulas is situated on the North Pacific coast of Costa Rica in the Guanacaste Province (10°20 N, 85°51 W). It was created in 1991 to protect the nesting beaches of leatherback turtles, together with associated mangrove and tropical dry forests (Consejo Nacional de Áreas de Conservación [CONAC] and Sistema Nacional de Áreas de Conservación [SINAC] 2019). The region has a tropical dry climate, receiving approximately 1,470 mm of rainfall during the wet season (May–October) and about 130 mm during the dry season (November–April), with temperatures ranging from 25–30°C throughout the year (https://www.imn.ac.cr/eninicio). Animal communities in the study area comprised large herbivores, mesocarnivores, and carnivores, as well as diverse resident and migratory bird assemblages (Proctor et al. 2025). The National Park protects a 125-m stretch behind the Park's beaches, from the mean high tide line to the vegetation. Behind the beach, the area is mainly characterized by a tropical dry forest. The Tamarindo Estuary, located at the southern end of the beach, is a wetland of international importance designated as a Ramsar site. Behind the Park, a buffer zone extends over 500 m (Figure 1) and is composed of tropical dry forest patches embedded within a matrix of urban areas and farmlands, with elevations ranging from 0 to 70 m above sea level. There are 3 sea turtle nesting beaches in the National Park: Playa Grande (3.6 km long), Ventanas (1 km long), which is located immediately north of Playa Grande, and Playa Langosta (1.3 km long). Playa Langosta is separated from the rest of PNMB by the town of Tamarindo (Piedra et al. 2007). We conducted this study in the area surrounding Playa Grande and Ventanas.

METHODS

Urban growth

To assess urban growth, we evaluated the change in urban development at PNMB over time. We retrieved satellite images (Landsat 5, 7, 8, 9) and Sentinel 2 collections from Google Earth Engine (Google, Mountain View, CA, USA) between January 1990, close to the establishment of PNMB, and May 2024. We selected only images with low cloud cover and excluded those with poor visibility. We counted the number of buildings (houses, hotels,

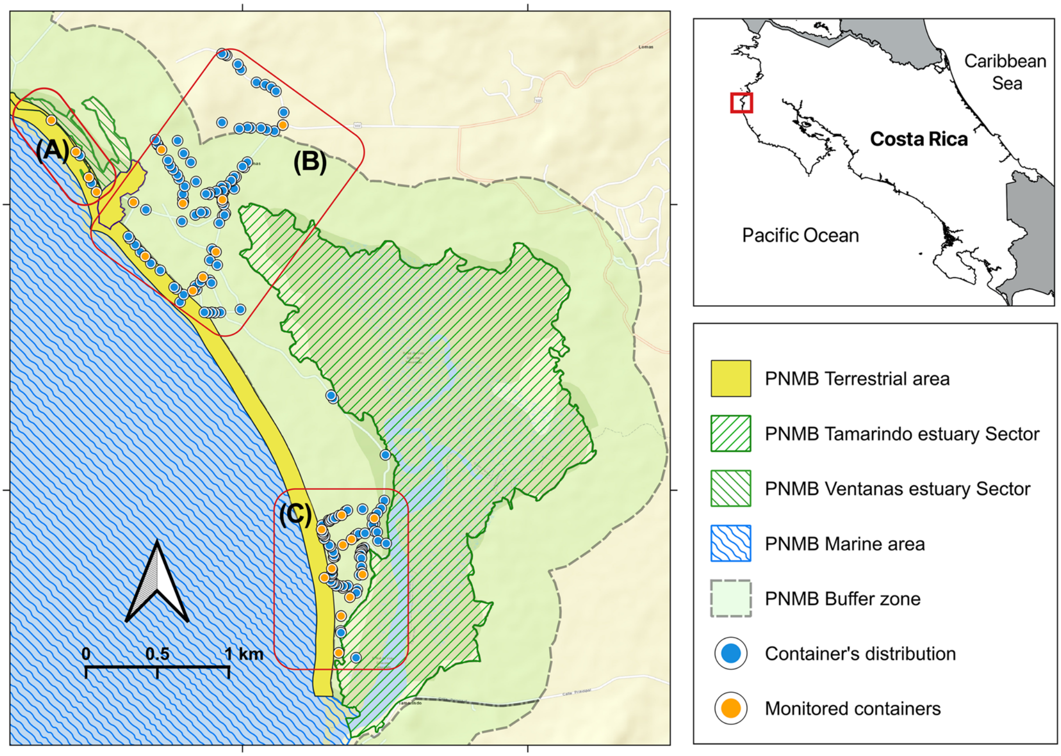

FIGURE 1 Las Baulas National Park (PNMB) on the Pacific coast of Costa Rica and garbage container distribution in 2021 along the terrestrial area of the park, buffer zone, and urban areas: A) Ventanas, B) Playa Grande North, and C) Playa Grande South.

restaurants, and other commercial buildings) per year in the main urban areas within the National Park and buffer zone: A) Ventanas, which is located behind Ventanas beach; B) Playa Grande North, located behind the first kilometer of Playa Grande beach toward the north; and C) Playa Grande South, located behind the last kilometer of Playa Grande toward the south (Figure 1). Playa Grande North and Playa Grande South are 1.4 km apart, separated by a strip of dry forest patches, mangroves, and farms, with no development. We used high-definition satellite imagery from Maxar Technologies (Maxar 2024) as control point images in 2003, 2005, 2010, 2016, 2019, 2021, 2022, and 2023 to verify the accuracy of building counts (Figure S2).

Wildlife access to garbage

We studied the interaction of wildlife with accessible PAFS in garbage containers at the 3 main urban concentration zones near the beach. We categorized the 3 urban zones by development level as low, medium, or high based on the total built-up area (m^2) covered by buildings: Playa Grande North was classified as high (144,549 m^2), Playa Grande South as medium (83,700 m^2), and Ventanas as low (6,190 m^2). To estimate the built-up area, we retrieved satellite images from July 2021 using Google Earth Engine, extracted polygons for all buildings in the study area, and automatically estimated the area covered by buildings using the free software QGIS (v3.34; QGIS Association, Grüt, Switzerland).

Prior to wildlife assessments with camera traps, we conducted systematic walking surveys throughout the urban areas surrounding PNMB to locate and categorize all trash containers. During these surveys, we recorded the presence or absence of a container at each site and, when present, classified containers by construction material. We identified 114 containers and grouped them into 39 mesh boxes (hereafter mesh), 10 cement sewer pipes (hereafter cement), 5 wood boxes (hereafter wood), 49 metallic boxes (hereafter metallic), and 11 plastic containers. We also identified 72 sites (e.g., houses, restaurants, hotels) without containers, where garbage was left in plastic bags (Figure S1). Overall, 102 sites (including both container and non-container sites) were located in Playa Grande North, 78 in Playa Grande South, and 6 in Ventanas.

To identify and characterize the effect of PAFS on the activity and detection of wildlife species, we selected 24 distinct containers (or sites with only plastic bags; Figure 1) and monitored them using infrared automatic camera traps (Moultrie Trail cameras®, AL, USA) between July and September 2021. These included 9 (9%), 11 (14%), and 4 (66%) sites monitored in Playa Grande North, Playa Grande South, and Ventanas, respectively (Table S1). We deployed each camera near a container over a full week, after which we downloaded the data and moved the camera to a different container to repeat the process. The number of cameras set simultaneously during a week varied between 2 and 5 (Table S1), depending on availability or logistical feasibility. We attached each camera to a tree at roughly 40 cm above the ground, pointing toward the garbage container. We set cameras to record videos when triggered via passive infrared sensor, with a delay of 30 seconds between triggers. As most tourist traffic occurred during the day, we set cameras to be active only at night (between 1700 and 0600, when it was dark).

For each video, we recorded the location, date, time, type of container, species, number of observed individuals, and whether or not the animal accessed the container. We considered each video as one detection independently of the group size. Following Montalvo et al. (2019), we classified a video as an independent record of a species if it met at least one of the following conditions: 1) if videos of the same species were taken at least 30 minutes apart; 2) if in consecutive videos of the same species we could identify different individuals (e.g., presence of scars, fur spots, sex); 3) if videos of other species separated videos of the same species. If none of these conditions were met, we considered videos as part of the same event and counted them as a single detection.

We assessed activity patterns using nonparametric kernel density functions based on hours of independent detections, using the activityDensity function in the overlap package (Agostinelli and Lund 2023). For this analysis, we included only raccoons, as more than 20 independent records are required for statistical robustness (Cruz-Díaz et al. 2024). We estimated access success by dividing the number of successful attempts (the observed animal successfully accessed the garbage container or extracted garbage) by the total number of attempts made per night. An attempt was recorded when an animal explored the container by sniffing around, manipulated it with its forepaws (in the case of raccoons), or jumped on it while looking for openings.

We fitted generalized linear mixed models to assess the influence of containers, and therefore PAFS, on wildlife. We used group sizes, number of detections per night, and access success as dependent variables. As fixed effects in the models, we included location of the container (Playa Grande North, Playa Grande South, or Ventanas), container type, and day of the week. We hypothesized that these independent variables could influence wildlife use of PAFS. In particular, the location of the container could reflect varying levels of urbanization, which may affect the amount and predictability of wasted food sources. Container type could facilitate or restrict access depending on its material and design. Weekday accounts for changes in food waste amounts and management by day of the week. In addition, we used Julian day as a random factor to account for temporal variability driven by specific conditions (e.g., weather, seasonal trends, or moon phases). We fitted models using the package glmmTMB (Brooks et al. 2017). We analyzed group size and number of detections per night using a log-link function (count data) and analyzed access success using a binomial distribution. Given our zero-heavy data (characteristic of camera-trap studies), we used zero-inflated generalized linear mixed models to analyze the number of detections per night.

To create the top model set, we used the dredge function from the MuMIn package (Bartoń 2013), which evaluates all subsets of a predefined global model and ranks them using Akaike's Information Criterion corrected for small sample sizes (AIC_c). We identified the best-fit model as the one with the lowest AIC_c value. Once we selected the best model, we ran Tukey's honestly significant difference (HSD) *post hoc* test with the emmeans and pairs functions from the emmeans package (Lenth 2025) to assess differences between the predictor groups. We used r.squaredGLMM (MuMIn) to calculate marginal (R^2m; variance explained by fixed effects) and conditional (R^2c; variance explained by fixed and random effects combined) coefficients. Because raccoons were the predominant species and detections of other species were low and sporadic, we could not include species as predictors or random effects to support species-level modeling. Consequently, models with group sizes as the dependent variable included only raccoon data, whereas those with the number of detections per night and access success as dependent variables included aggregated detections of all identified species.

Predation of sea turtle nests

For nest predation, we obtained data from the sea turtle research project at Playa Grande and Ventanas. We used all nest data from Playa Grande, including nests located in the undeveloped 1.4-km section between the 2 urban zones, and data from Ventanas. Additionally, because the number of leatherback turtle and green turtle nests reported as predated at PNMB was very low ($n < 5$, both species together), we assessed the change in predation levels using only olive ridley turtle nests, which are much shallower (~47 cm vs. ~82 cm in leatherback and ~68 cm in green turtles; Santidrián Tomillo et al. 2017) and, therefore, are more exposed and easier to find by predators.

The study of olive ridley turtles started in 2011–2012 (Dornfeld et al. 2015). Every season (October–March), we conducted nightly beach patrols to locate nesting turtles and marked a subset of *in situ* nests. To evaluate changes in nest predation over time, we included data from nesting seasons between the 2011-2012 season and the 2017-2018 season. Prior to the 2017-2018 season, the turtle research team selectively relocated olive ridley clutches at risk of inundation, poaching, or other threats, excluding predation. However, as the number of olive ridley nests found predated on the beach greatly increased in seasons 2015-2016 and 2016-2017, researchers started relocating all clutches they were able to encounter and handle (>80% of all clutches laid) to a beach hatchery to reduce predation, starting in 2017-2018 (Rutledge et al. 2024). Consequently, we excluded seasons after 2017-2018 from the predation analysis as the sample size was too small (few nests remained on the beach while the hatchery was in operation). We recorded a nest as predated if it had been dug up and eggshell fragments or hatchling remains were visible on the surface. Observers usually recorded predation events on marked nests during morning surveys or night patrols and confirmed predator identity from tracks or direct observations. Raccoons were the main species found to prey on egg clutches during the study period at PNMB (91% of instances in which the predator was identified), although some nests were also dug by dogs (7%). We recorded 3 additional clutch-predation events, each at a different nest, attributable to a crested caracara (*Caracara plancus*), a white-nosed coati (*Nasua narica*), and a ghost crab (*Ocypode gaudichaudii*), respectively. No other species were found to prey on eggs, but different species of birds and crabs were previously identified to prey on sea turtle hatchlings at PNMB (Santidrián Tomillo et al. 2010).

We estimated the percentage of predated nests by dividing the number of marked *in situ* nests that were predated by the total number of marked *in situ* nests each season. We additionally estimated the percentage of relocated clutches, as it can reflect the impact of predation risk on clutch management. Upon relocation, we always annotated the reason for relocation, which, since 2017-2018, was due to predation risk in >90% of clutches each season. To assess how predation pressure affected clutch relocation, we divided the number of relocated clutches by the total number of body pits (shallow depressions in the sand left by nesting females after laying) recorded during the same time period the relocation program was in operation (October to December) between 2010-2011 and 2023-2024 seasons. We excluded from analysis nesting seasons when the hatchery was not operating as normal because of the COVID pandemic (2020-2021 and 2021-2022).

To explore potential relationships between urban growth and nest predation, we fitted a generalized linear model. We used *in situ* nest records from the 2011-2012 and 2017-2018 seasons and classified each nest as predated (1) or not predated (0). Full models included 3 predictors: 1) the number of buildings counted per year in the whole study area; 2) the number of buildings within 32 ha around each nest (hereafter buildings near the nest), which has been previously described as the mean area used by raccoons to exploit PAFS in a different National Park in Costa Rica (Carrillo and Vaughan 1993); and 3) the distance to the nearest garbage container. To determine the number of buildings near a nest, we used satellite imagery. Using Google Earth, we established a 32-ha circle around each nest in each season and determined the number of buildings in it. We did not include Ventanas in this analysis because the sea turtle monitoring effort was lower there than at Playa Grande.

We tested all models for deviance using null and residual deviances to verify their adjustment with the Dsquared function from the modEvA package (Barbosa et al. 2013). After fitting the models, we tested for data dispersion and uniformity using the aods3 and DHARMa packages (Lesnoff and Lancelot 2022, Hartig et al. 2024) and verified that all model assumptions were met using the diagnostic graphs of deviance residuals. We conducted all statistical tests with an α = 0.05 in R Statistical Software (v4.3.2; R Core Team 2023).

RESULTS

Urban growth and predation of sea turtle nests

The number of buildings in the study area doubled from 47 units in 1991 to 94 units in 2001. Growth accelerated over the following 2 decades, reaching 292 units by 2019 (>6 times the 1991 baseline) and 487 units by 2024 (>10 times the 1991 baseline; Figure 2A). Of the 3 areas, Playa Grande North experienced the most intense development, rising from 9 building units in 1991 to 311 units in 2024. Playa Grande South grew from 37 to 168 building units over the same time period, and Ventanas grew from 3 to 8 building units.

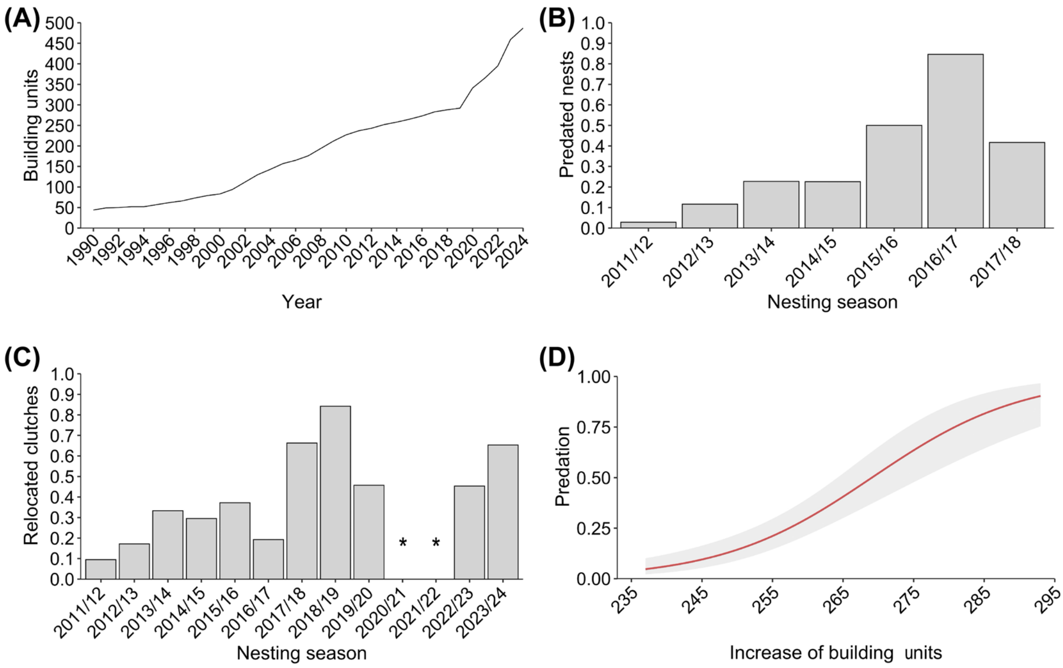

FIGURE 2 Increases in A) building units constructed per year, B) proportion of predated nests, C) proportion of relocated nests, and D) relationship between the number of buildings and proportion of predated olive ridley turtle nests in Las Baulas National Park, Costa Rica, with the 95% confidence intervals (gray area).

Wildlife access to garbage

Our cameras operated over 166 cumulative trap nights in the 3 urban areas during the study period. We identified 8 species that interacted with garbage containers from 211 independent videos: lowland paca (*Cuniculus paca*), nine-banded armadillo (*Dasypus novemcinctus*), Virginia opossum (*Didelphis viginiana*), gray fox (*Urocyon cinereoargenteus*), spotted skunk (*Spilogale angustifrons*), hooded skunk (*Mephitis macroura*), coyote, and raccoon (Figure 3).

Raccoons had the highest number of independent detections ($n = 168$), followed by coyotes ($n = 16$) and hooded skunks ($n = 7$). Raccoons were also the most widely distributed species, being detected at all 3 studied sites (Table 1). Raccoons exhibited 2 peaks of activity during the night, accounting for 70% ($n = 115$) of their detections. Activity increased shortly after sunset, with 36% ($n = 60$) of detections recorded between 1800 and 2100; activity rose again after midnight, with 34% ($n = 57$) of detections between 0100 and 0400 (Figure 4). The 2 activity peaks occurred at 1900 and 0200, indicating increased activity in the hours after sunset and before sunrise. Their group sizes varied between 1 and 4 individuals across locations. The model that best explained the variability in group size only included the intercept (Table 2), suggesting that day of the week, location, and type of container did not influence group size. The second-best model was separated by 2.75 AIC_c points (Table 2) and included location as a predictor; however, we did not find evidence for a relationship between the location variable and group size ($X^2_2 = 1.61$, $P = 0.45$). Across all models, the conditional and marginal coefficients were identical (Table 2), indicating that the random (date) effects explain zero variance and provide no additional predictive power.

Concerning the number of detections per night, the model with the lowest AIC_c included location and type of container as predictors, and both had strong evidence of an effect (location: $X^2_2 = 9.45$, $P < 0.001$; container type: $X^2_5 = 34.22$, $P < 0.001$; Table 2). Mean (±SE) number of detections per night was higher at Playa Grande North (4.2 detections ± 0.8) and Playa Grande South (3.9 ± 1.1) than at Ventanas (2.2 ± 0.6, Tukey's HSD $P < 0.05$; Figure 5A), indicating greater wildlife activity at containers within developed areas. Additionally, the number of detections per night was higher around cement (6.4 detections ± 2.1) and plastic (4.3 ± 1.7) containers than around the other types (Tukey's HSD $P < 0.05$; Figure 5B). The lowest number of detections per night occurred around metal containers (1.9 detections ± 0.3); although, the number of detections at metal containers was similar to detections at wood and mesh containers or places without containers (Tukey's HSD $P > 0.05$). The conditional regression coefficient was larger ($R^2 = 0.73$) than the marginal coefficient ($R^2 = 0.31$), indicating that the random factor (date) explained a larger proportion of the variance.

The model that best explained variability in access success included type of container as the only factor with evidence of an effect ($X^2_5 = 23.85$, $P \leq 0.001$; Table 2). Access success was higher in areas with no containers (93.7% ± 3.3) and with plastic containers (73.3 ± 8.1) than for the rest (Tukey's HSD, $P \leq 0.001$; Figure 5C). Access success was relatively higher in cement (58.7% ± 9.3) and mesh (54.15 ± 15.0) containers, and lower in metallic (35.1 ± 12.3) and wood (22.4 ± 8.2) containers, but there was no statistical evidence of differences between these containers (Tukey's HSD $P > 0.05$ in all cases; Figure 5C). Additionally, the conditional and marginal coefficients were equal in all models, indicating that the random factor (date) explained no variance.

Predation of sea turtle nests

Regarding predation, we monitored 184 *in situ* olive ridley nests between 2011–2012 and 2017–2018, of which 10% ($n = 18$) were located in Ventanas, 19% ($n = 34$) in the beach section corresponding to Playa Grande North, 26% ($n = 47$) in the beach section corresponding to Playa Grande South, and 46% ($n = 84$) along the 1.4-km stretch of beach between Playa Grande North and South that had no buildings behind the beach. The percentage of predated olive ridley nests increased from 3% in 2011–2012 to 85% in 2016–2017 (Figure 2B). During that time, nests were most often predated along the 1.4-km stretch of beach between Playa Grande North and South (49%), followed by the section of beach in front of Playa Grande South (18%), Ventanas (18%), and Playa Grande North (16%).

FIGURE 3 Wildlife species identified accessing garbage containers in the surrounding areas of Las Baulas National Park, Costa Rica, in 2021: A) coyote (*Canis latrans*), B) paca (*Cuniculus paca*), C) opossum (*Didelphis viginiana*), D) hooded skunk (*Mephitis macroura*), E) spotted skunk (*Spilogale putorius*), F) gray fox (*Urocyon cinereoargenteus*), G) nine-banded armadillo (*Dasypus novenmcinctus*), and H) northern raccoon (*Procyon lotor*).

TABLE 1 Number and percentage of detections for each species at Ventanas, Playa Grande North, and Playa Grande South in Las Baulas National Park, Costa Rica, 2021, and the maximum group size seen in interaction with garbage containers.

Common name	Scientific name	Detections (%)	Max. group size	Urban zone[a]
Paca	*Cuniculus paca*	2 (0.7%)	1	V
Nine-banded armadillo	*Dasypus novemcinctus*	3 (1.0%)	1	PGN
Virginia opossum	*Didelphis virginiana*	3 (1.0%)	1	PGN, PGS
Gray fox	*Urocyon cinereoargenteus*	4 (1.5%)	2	PGN
Spotted skunk	*Spilogale angustifrons*	6 (2.0%)	1	PGN
Hooded skunk	*Mephitis macroura*	7 (2.5%)	1	PGN, PGS
Coyote	*Canis latrans*	18 (7.0%)	2	PGN, PGS
Northern raccoon	*Procyon lotor*	222 (84.0%)	4	V, PGN, PGS

[a] V = Ventanas, PGN = Playa Grande North, PGS = Playa Grande South.

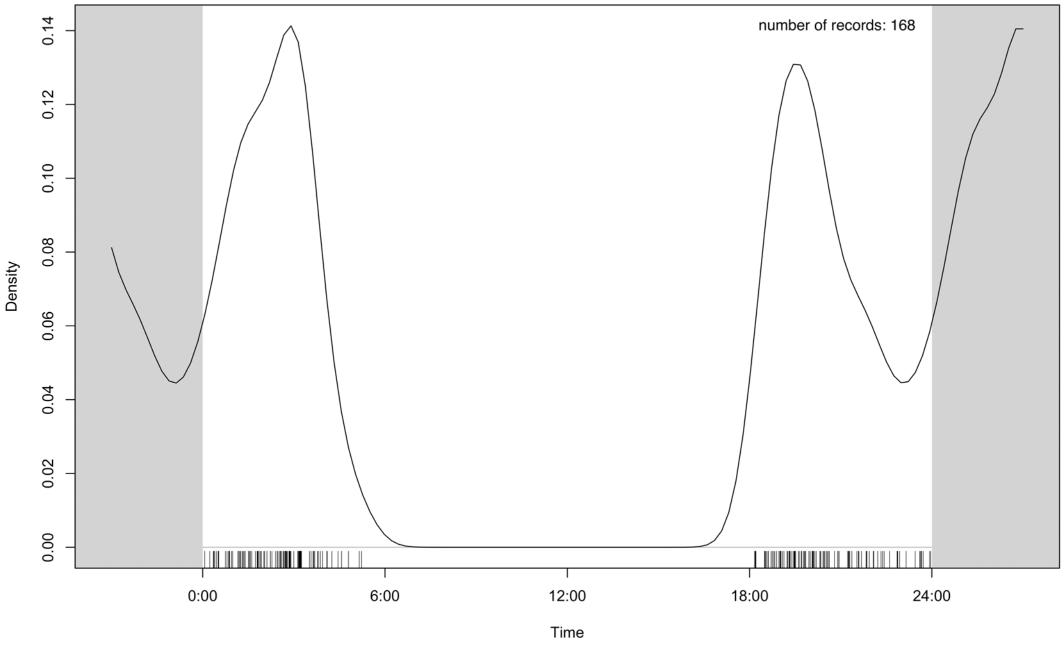

FIGURE 4 Kernel density estimates of nocturnal activity patterns for northern raccoons (*Procyon lotor*) interacting with garbage containers at Las Baulas National Park, Costa Rica, over the study period in 2021. No data were obtained between 0600 and 1800. Kernel density is the relative probability of an animal being active at a specific time.

Additionally, 336 olive ridley nests were relocated to the hatchery between 2010–2011 and 2023–2024. The proportion of relocated clutches increased after the 2016–2017 season, reaching a peak of 84% in 2018–2019 (Figure 5C).

When analyzing the effect of urban growth on nest predation, we excluded distance to the nearest container because of its strong negative correlation with the number of buildings near nests ($r = -0.74$) and because the model had a poorer fit (greater AIC_c value) when it was included. We found that the number of buildings in the whole

TABLE 2 Model selection results assessing the influence of container types, urban zones, and day of the week on raccoon group size, and detections per night and access success for all wildlife species in Las Baulas National Park, Costa Rica, 2021.

Model	df	AIC_c[a]	ΔAIC_c[b]	Weight	R^2m[c]	R^2c[d]
Group size						
Intercept	3	210.4	0.00	0.79	0.00	0.00
Urban zone	5	213.2	2.75	0.20	0.23	0.23
Container	8	220.0	9.57	0.01	0.02	0.02
Container + urban zone	10	221.8	11.4	0.00	0.07	0.07
Day of the week	9	222.0	11.5	0.00	0.04	0.04
Urban zone + day of the week	11	225.7	15.3	0.00	0.06	0.06
Container + day of the week	14	234.1	23.7	0.00	0.06	0.06
Container + urban zone + day of the week	16	237.3	26.9	0.00	0.12	0.12
Detections per night						
Container*** + urban zone**	9	485.1	0.00	0.87	0.31	0.73
Container***	11	489.2	4.08	0.11	0.26	0.71
Container + day of the week	15	493.1	7.99	0.02	0.37	0.72
Container*** + urban zone + day of the week	17	497.8	12.71	0.00	0.42	0.73
Urban zone*	6	502.9	17.77	0.00	0.08	0.67
Intercept	4	503.1	17.99	0.00	0.00	0.66
Day of the week	10	509.3	24.14	0.00	0.20	0.66
Urban zone* + day of the week	12	510.8	25.65	0.00	0.25	0.68
Access success						
Container**	9	−278.8	0.0	0.81	0.44	0.44
Intercept	4	−275.7	3.09	0.12	0.00	0.00
Urban zone	6	−274.8	3.97	0.04	0.15	0.15
Container* + urban zone	11	−273.5	5.22	0.03	0.44	0.44
Container** + day of the week	15	−266.9	11.87	0.00	0.53	0.53
Urban zone + day of the week	12	−264.8	13.91	0.00	0.32	0.32
Day of the week	10	−264.6	14.16	0.00	0.16	0.16
Container* + urban zone + day of the week	17	−260.9	17.84	0.00	0.54	0.54

Note: Fixed effects with an asterisk (*) have a statistically significant influence on the response: $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.

[a] Akaike's Information Criterion corrected for small samples.

[b] Difference of AIC_c values between ranked models.

[c] Marginal R^2 (variance explained by fixed effects only in mixed models).

[d] Conditional R^2 (variance explained by fixed + random effects in mixed models).

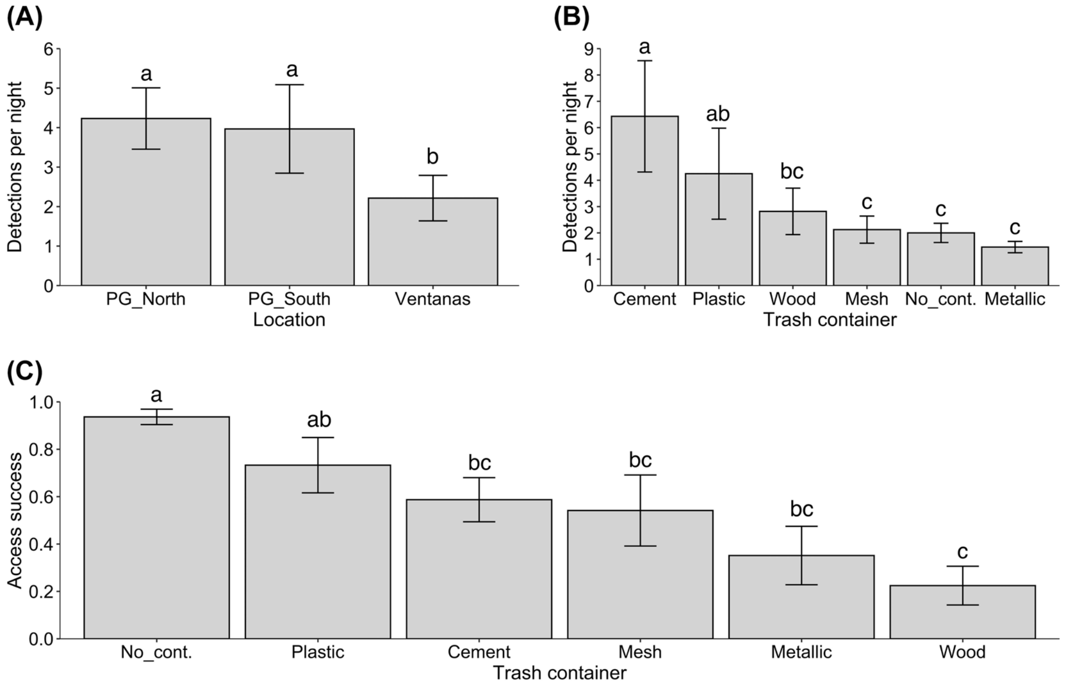

FIGURE 5 Number of detections per night (±SE) in Las Baulas National Park, Costa Rica, 2021, across A) urban areas (Playa Grande North [PG_North], Playa Grande South [PG_South], or Ventanas) and B) garbage container type or no container (No_cont.; e.g., plastic bag), and C) access success to the containers. Bars with different letters were significantly different from one another based on multiple *post hoc* comparisons using Tukey's honestly significant difference (HSD) test with alpha = 0.05.

study area influenced the number of predated nests ($X^2 = 56.62$, $P < 0.01$), indicating a possible association between predation and urban growth (Figure 5D). Conversely, we did not find evidence that the number of buildings surrounding the nest had a relationship with predated nests ($X^2 = 2.45$, $P = 0.13$), indicating that buildings in the typical range area of raccoons may not influence predation.

DISCUSSION

Our study indicated that urban growth around PNMB had an impact on native wildlife species. We found that 8 different species exploited PAFS from garbage containers in the urban areas of PNMB. Although we did not directly quantify changes in the availability of PAFS, our results showed that wildlife frequently interacted with garbage containers and were often successful in accessing them, suggesting that these resources are readily available. Access to PAFS may have indirectly contributed to a rise in sea turtle nest predation by favoring larger raccoon populations, thereby threatening the conservation target species.

Urban growth and wildlife access to garbage

Costa Rica is known for a well-established network of national parks and other protected areas. However, if the number of visitors and residents in an area exceeds manageable levels near protected areas, there could be a detrimental effect on wildlife, counteracting conservation efforts (Mcdonald et al. 2008). We found that PNMB, and especially its buffer zone, experienced an exponential increase in urban growth since the Park was established in the early 1990s, with an acceleration in the growth rate in recent years (Figure 5A). Associated with this development, native species have learned to use garbage as food sources within the protected area. In addition to raccoons, some of the species recorded, also known as PAFS exploiters in other regions (Fedriani et al. 2001, Wright et al. 2012, Larson et al. 2015, Degregorio et al. 2023), are recognized predators of sea turtle nests. These included coyotes, armadillos, gray foxes, and Virginia opossums (Stancyk 1982, Woolard et al. 2004, Gandu et al. 2013, Méndez-Rodríguez and Álvarez-Castañeda 2016). Although we have never observed these species predating on sea turtle nests at PNMB, they can be considered potential predators.

Our findings indicate that raccoons were the primary species exploiting PAFS across the studied areas. Their higher number of detections is likely due to their synanthropic behavior (the ability to live near humans) and dietary flexibility (Prange and Gehrt 2004, Gross et al. 2012), which enable raccoons to adapt to and successfully exploit urban areas. When evaluating the activity of raccoons, we found that this species was most active after sunset and before sunrise, consistent with nocturnal activity reported for urban populations in other regions (Mayer et al. 2023, Proudman and Allen 2025). Their activity pattern may be a response to optimize resource exploitation and reduce encounters with competitors or predators (Botts et al. 2020, Gallo et al. 2022, Mims et al. 2022). Access to PAFS can further influence wildlife activity patterns. For example, at Manuel Antonio National Park, a protected area with the highest number of tourist visits in Costa Rica, raccoons shifted from being mainly crepuscular (Carrillo 1990) to diurnal (Ferrera 2016) in response to tourist activity and food availability. However, this shift has not been observed at PNMB, where the number of tourists is much lower than at Manuel Antonio.

The higher number of detections in more developed areas may reflect increased wildlife activity driven by greater resource availability. Elevated detections could also indicate a higher concentration of species that exploit garbage in urbanized areas. Anthropogenic food waste in garbage is often predictable and energy-rich, which can improve the nutritional condition of raccoons and other generalist foragers (Demeny et al. 2019), thereby promoting higher survival, reproduction, and ultimately population growth (Graser et al. 2012). For instance, raccoon and coyote populations in urban areas can reach densities 4–12 times greater than those in rural areas (Fedriani et al. 2001, Prange et al. 2003, Gehrt 2004), which could contribute to the higher number of detections observed. Although our detection patterns may be related to these dynamics, additional research is needed to quantify wildlife densities and resource availability across PNMB urban gradients and to assess how these factors relate to variation in detection numbers.

The type of container also influenced the number of detections and access success (Figure 4B, C). This could be explained by the storage capacity or the design of the container (Figure S1), which could facilitate garbage extraction more easily for some types than for others. For example, the amount of waste seemed higher during peak tourist visitation and housing occupation, when the capacity of containers was often exceeded (K. E. Cordero, Menéndez Pelayo International University, personal observation). In addition, wood containers were accessed less successfully than other containers, indicating that their design may be more effective. However, wood containers are likely not optimal because they could deteriorate rapidly in coastal and tropical conditions. In any case, container replacement should start with those that had the poorest performance (those with a higher number of detections and extraction success). At PNMB, new wildlife deterrent containers are being tested as a proof of concept. These containers are made of anti-corrosive metal sheets with ample storage capacity and self-closing doors. They aim to reduce wildlife access while facilitating waste disposal and cleaning.

Although we found that the location and type of container influenced the number of detections per night, the random effect (date) explained more variance than the fixed effects (Table 2). This suggested that other factors not tested here, such as specific environmental conditions, moon phase, or holiday occurrences, may have influenced the number of detections. For example, Nix et al. (2018) found that temperature, precipitation, and the intensity of moonlight also influenced the detections of nocturnal mammals. Our study was conducted during the rainy season, and the occurrence and intensity of rainfall events could have affected animal movement. Additionally, moonlight can also influence the movement of species that aim to prey on or avoid predation (Chitwood et al. 2020).

Occasionally, the Municipality was unable to collect the garbage, and sometimes plastic bags were left on the road outside containers. Surprisingly, the number of detections per night in areas with no containers was low despite these being easily accessible (Figure 4C). This may be because their occurrence was less predictable, reinforcing that predictability may be a more important component than resource abundance, and supporting the concept of PAFS as drivers of animal behavior (Oro et al. 2013). In addition, when plastic bags are encountered, wildlife may rapidly exploit all available resources, possibly reducing the attraction for other predators.

We did not detect an effect of location, day of the week, or type of container on the group size of raccoons. Raccoons typically form stable groups of 3-5 members, and this seems to be the optimal size for being competitive for space, resources, and mates (Gehrt et al. 2008, Pitt et al. 2008). Raccoons at PNMB made groups of similar numbers. Thus, a greater abundance of PAFS may result in an increase in the number of groups rather than in the size of the groups (Gehrt 2004).

Sea turtle nest predation

Along with urbanization, the occurrence of PAFS and the high access success around poorly designed containers likely allowed raccoons to increase their population size at the National Park. As a result, they not only became the primary garbage exploiter at PNMB but were also confirmed as the main predator of sea turtle nests during our study.

Our results indicated that the number of buildings constructed annually could possibly be associated with an increase in nest predation (Figure 5D). If this were the case, the rapid effect of development on predation could be explained by the rapid maturity of raccoons (reaching sexual maturity at ~10–12 months) and their high reproductive rates, which can produce up to 7 pups per litter (Fritzell 1978, Troyer et al. 2014, Ishiguro 2023). These characteristics enable raccoon populations to expand quickly in response to new anthropogenic resources. However, at this time, our data do not allow us to determine a direct causal link between urban development and nest predation. The number of buildings serves only as a proxy for urbanization and human disturbance and may not directly capture the mechanisms driving predation. Thus, future studies considering habitat use, distribution range, and raccoon movements between urban areas and the beach might help to establish a direct link between urbanization and predation. In addition, other factors not considered in this study, such as large predator abundance, food availability, or tourist occupation, may also have influenced raccoon behavior and densities and potentially, nest predation rates. Even with these limitations, the patterns we observed suggest that continued development, particularly in the absence of effective waste management within PNMB, could exacerbate impacts on wildlife such as sea turtles. Similar dynamics have also been documented in Florida, USA, where habitat loss due to urbanization, availability of predictable anthropogenic food subsidies, and the decline of large carnivores have facilitated mesocarnivore (i.e., raccoons) population growth. As a consequence, raccoons were responsible for ≥80% predation of loggerhead turtle nests across several nesting seasons (Bain et al. 1997, Engeman et al. 2003).

We did not find evidence of an effect of the number of buildings near a nest on chances of predation. This could be due to the exploratory nature of raccoons, which move over large areas (Prange et al. 2004, Beasley et al. 2007), and the unpredictable locations of sea turtle nests. Welicky et al. (2012) found that the spatial and temporal variability of sea turtle nests greatly influenced nest predation. However, because olive ridley nests do not concentrate in a particular area of PNMB beach and the number of nests is currently low (1–5 nests per night during peak season) and extends over several kilometers, the most efficient strategy for raccoons may be patrolling the beach in search of sea turtle eggs. During the study period, about 46% of monitored olive ridley nests were located along the 1.4-km stretch of beach between Playa Grande North and South, and this section accounted for 49% of all nest predation events. Therefore, it appears that subsidized predators move along the beach and prey in areas where nests are concentrated. The combined resource availability and the high caloric value of sea turtle eggs and hatchlings (Bouchard and Bjorndal 2000) may make displacements cost-effective.

Finally, green and leatherback nest predation is very low at PNMB because the eggs of these species are buried at greater depths than those of olive ridley turtles (Santidrián Tomillo et al. 2017). However, hatchlings of all species could be potentially predated during emergence by raccoons or other species, and future studies should also attempt to assess the effects of predation on hatchlings. Likewise, species such as coyotes may be capable of digging deeper than raccoons. Although coyotes are frequent predators of loggerhead and olive ridley turtle nests, which are shallow (Méndez-Rodríguez and Álvarez-Castañeda 2016, Lovemore et al. 2020), they have also been documented occasionally preying on green and leatherback turtle nests (Drake et al. 2003, Engeman et al. 2005). Hence, while raccoons currently pose the primary threat to sea turtle nests, other opportunistic species identified in this study could also increase in number and prey on nests.

MANAGEMENT IMPLICATIONS

The proliferation of raccoons and other wildlife facilitated by PAFS underscores the need for active management at PNMB. Although lethal raccoon control has been implemented in other regions (e.g., Florida, USA), this approach triggered unintended cascading effects. Secondary predators, particularly the ghost crab (*Ocypode quadrata*), increased in abundance, further intensifying sea turtle nest predation (Barton 2005, Barton and Roth 2008). Alternatively, long-term strategies that reduce PAFS could avoid this side effect by promoting natural predator regulation. For example, in the Big Basin Redwoods State Park (California, USA), limiting PAFS reduced populations of Steller's jays (*Cyanocitta stelleri*), a predator of endangered seabirds (Brunk et al. 2021).

Enhancing waste management through well-designed containers (sufficient capacity and self-closing lids), along with organic waste reduction and visitor education, would improve conservation outcomes while creating an experimental framework to test the direct effects of development. By monitoring predator responses to decreased PAFS, managers can directly assess how PAFS availability influences raccoon population dynamics and nest predation rates. For example, studies using cameras to determine population size (Davis et al. 2025), in combination with radio telemetry (habitat use and movements between urban areas and nesting beaches), could help identify behavioral adaptations and population responses of raccoons linked to PAFS reduction. On the other hand, reducing PAFS could initially increase raccoon pressure on sea turtle nests, as animals seek alternative food sources. Thus, improved garbage management should be accompanied by direct nest protection measures (e.g., *in situ* nest caging, hatchery relocation) to safeguard clutches and enhance hatchling production as raccoon populations decrease.

Finally, urban development has expanded in and around PNMB despite its designation as a National Park. Since 1991, changes in construction restrictions by different governments have allowed an intermittent but exponential growth that has affected wildlife, and especially the conservation target species. Preventing further development is therefore essential, and a key management strategy to protect wildlife at PNMB, to continue exploiting the ecotourism business promoted by the country.

ACKNOWLEDGEMENTS

We thank the Playa Grande field biologists, volunteers, and the Leatherback Trust staff who assisted with the data collection and logistics during the study period. We also thank the Playa Grande community, National Park Rangers, and local businesses for their assistance in distributing the generated information. We thank the Tempisque Conservation Area of the Ministry of Environment and Energy for granting the necessary research permits. This study took place within the program "Maximizing hatchling output of leatherback turtles in Costa Rica," funded by the National Fish and Wildlife Foundation (NFWF) and was supported and administered by The Leatherback Trust. The Earthwatch Institute, Purdue University, and The Leatherback Trust provided funding for the long-term monitoring study of sea turtles.

CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

ETHICS STATEMENT

No live animals were captured or handled as part of this research. Our study synthesized wildlife animal interactions with garbage in urban areas and the indirect effects on an endangered species. Data were collected and managed by The Leatherback Trust. All monitored containers were located in the public zone, outside of private properties, and studied under Tempisque Conservation Area (ACT) research permission (ACT-OR-DR-082-2021).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Keilor E. Cordero-Umaña https://orcid.org/0000-0002-4874-9577
Adam Yaney-Keller https://orcid.org/0000-0003-1538-664X
Javier López Navas https://orcid.org/0000-0001-6684-4538
Frank V. Paladino https://orcid.org/0000-0002-6452-0086
Pilar Santidrián Tomillo https://orcid.org/0000-0002-6895-7218

REFERENCES

Abreu-Grobois, A., and P. Plotkin. 2008. *Lepidochelys olivacea*. The IUCN Red List of Threatened Species 2008:e.T11534A3292503.

Agostinelli, C., and U. Lund. 2023. R package "circular": circular statistics (version 0.5-0). https://CRAN.R-project.org/package=circular.

Bain, R. E., S. D. Jewell, J. Schwagerl, and B. S. Neely Jr. 1997. Sea turtle nesting and reproductive success at the Hobe Sound National Wildlife Refuge (Florida), 1972–1995. U.S. Fish and Wildlife Service, ARM Loxahatchee NWR, Boynton Beach, Florida, USA.

Barbosa, A. M., R. Real, A. R. Muñoz, and J. A. Brown. 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. Diversity and Distributions 19:1333–1338. https://doi.org/10.1111/ddi.12100

Barton, B. T. 2005. Cascading effects of predator removal on the ecology of sea turtle nesting beaches. Thesis, University of Central Florida, Orlando, USA. https://stars.library.ucf.edu/etd/280

Barton, B. T., and J. D. Roth. 2008. Implications of intraguild predation for sea turtle nest protection. Biological Conservation 141:2139–2145. https://doi.org/10.1016/J.BIOCON.2008.06.013

Bartoń, K. 2013. MuMIn: multi-model inference (R package version 1.48.11). https://CRAN.R-project.org/package=MuMIn.

Bateman, P. W., P. A. Fleming, T. Fleming, and S. Le Comber. 2012. Big city life: carnivores in urban environments. Journal of Zoology 287:1–23. https://doi.org/10.1111/J.1469-7998.2011.00887.X

Beasley, J. C., T. L. Devault, and O. E. Rhodes. 2007. Home-range attributes of raccoons in a fragmented agricultural region of Northern Indiana. Journal of Wildlife Management 71:844–850. https://doi.org/10.2193/2006-022

Botts, R. T., A. A. Eppert, T. J. Wiegman, A. Rodriguez, S. R. Blankenship, E. M. Asselin, W. M. Garley, A. P. Wagner, S. E. Ullrich, and G. R. Allen. 2020. Circadian activity patterns of mammalian predators and prey in Costa Rica. Journal of Mammalogy 101:1313–1331. https://doi.org/10.1093/jmammal/gyaa103

Bouchard, S., and K. A. Bjorndal. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. Ecology 81:2305–2313. https://doi.org/10.1890/0012-9658(2000)081[2305:STABTO]2.0.CO;2

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400. https://doi.org/10.32614/RJ-2017-066

Brunk, K. M., E. H. West, M. Z. Peery, and A. M. Pidgeon. 2021. Reducing anthropogenic subsidies can curb density of overabundant predators in protected areas. Biological Conservation 256:109081. https://doi.org/10.1016/j.biocon.2021.109081

Carey, M. P., B. L. Sanderson, K. A. Barnas, and J. D. Olden. 2012. Native invaders–challenges for science, management, policy, and society. Frontiers in Ecology and the Environment 10:373–381. https://doi.org/10.1890/110060

Carrillo, E. 1990. Patrones de movimiento y hábitos alimenticios del mapachín (*Procyon lotor*) en el Parque Nacional Manuel Antonio, Costa Rica. Thesis, Universidad Nacional, Heredia, Costa Rica.

Carrillo, E., and C. Vaughan. 1993. Variation in the behavior of *Procyon* spp. (Carnivora: Procyonidae) due to the presence of tourists in a protected area of Costa Rica. Revista de Biología Tropical 41:843–848. https://revistas.ucr.ac.cr/index.php/rbt/article/view/24113

Chitwood, M. C., M. A. Lashley, S. D. Higdon, C. S. De Perno, and C. E. Moorman. 2020. Raccoon vigilance and activity patterns when sympatric with coyotes. Diversity 12(9):341. https://doi.org/10.3390/D12090341

Consejo Nacional de Áreas de Conservación [CONAC] and Sistema Nacional de Áreas de Conservación [SINAC]. 2019. Oficialización de los límites del Parque Nacional Marino Las Baulas de Guanacaste, Sistema Nacional de Áreas de Conservación, Resolución R-SINAC-CONAC-29-2019. http://www.pgrweb.go.cr/scij/Busqueda/Normativa/Normas/nrm_texto_completo.aspx?param1=NRTC&nValor1=1&nValor2=89050&nValor3=116690&strTipM=TC. Accessed 21 Oct 2024.

Cornhill, C. 2021. Depredation of olive ridley and loggerhead turtle clutches on beaches with and without predator management. Thesis, Purdue University, Fort Wayne, Indiana, USA.

Cruz-Díaz, J. C., M. Villalobos, V. H. Montalvo, C. Sáenz-Bolaños, T. K. Fuller, and E. Carrillo. 2024. Habituation of wildlife to ecotourism: a COVID-19 lockdown experiment in Corcovado National Park, Costa Rica. Wildlife Letters 2(1):5–16. https://doi.org/10.1002/wll2.12032

Davis, A. J., W. C. Dixon, R. B. Chipman, A. T. Gilbert, J. E. Hill, J. C. Beasley, O. E. Rhodes, and G. Dharmarajan. 2025. Raccoon density estimation from camera traps for raccoon rabies management. Journal of Wildlife Management 89:e22701. https://doi.org/10.1002/jwmg.22701

Degregorio, B. A., M. R. McElroy, and E. P. Johansson. 2023. Occupancy and activity patterns of nine-banded armadillos (*Dasypus novemcinctus*) in a suburban environment. Diversity 2023:907. https://doi.org/10.3390/d15080907

Demeny, K., M. McLoon, B. Winesett, J. Fastner, E. Hammerer, and J. N. Pauli. 2019. Food subsidies of raccoons (*Procyon lotor*) in anthropogenic landscapes. Canadian Journal of Zoology 97:654–657. https://doi.org/10.1139/cjz-2018-0286

Ditchkoff, S. S., S. T. Saalfeld, and C. J. Gibson. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. Urban Ecosystems 9:5–12. https://doi.org/10.1007/S11252-006-3262-3

Dornfeld, T. C., N. J. Robinson, P. Santidrián Tomillo, and F. V. Paladino. 2015. Ecology of solitary nesting olive ridley sea turtles at Playa Grande, Costa Rica. Marine Biology 162:123–139. https://doi.org/10.1007/S00227-014-2583-7

Drake, D. L., J. E. Behm, M. A. Hagerty, P. A. Mayor, S. J. Goldenberg, and J. R. Spotila. 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.

Engeman, R. M., R. E. Martin, B. Constantin, R. Noel, and J. Woolard. 2003. Monitoring predators to optimize their management for marine turtle nest protection. Biological Conservation 113:171–178. https://doi.org/10.1016/S0006-3207(02)00295-1

Engeman, R. M., R. E. Martin, H. T. Smith, J. Woolard, C. K. Crady, S. A. Shwiff, B. Constantin, M. Stahl, and J. Griner. 2005. Dramatic reduction in predation on marine turtle nests through improved predator monitoring and management. Oryx 39:318–326. https://doi.org/10.1017/S0030605305000876

Etter, D. R., K. M. Hollis, T. R. Van Deelen, D. R. Ludwig, J. E. Chelsvig, C. L. Anchor, and R. E. Warner. 2002. Survival and movements of white-tailed deer in suburban Chicago, Illinois. Journal of Wildlife Management 66:500–510. https://doi.org/10.2307/3803183

Food and Agriculture Organization of the United Nations [FAO]. 2011. Global food losses and food waste: extent, causes and prevention. Pages 1–23 *in* J. Gustavsson, C. Cederberg, U. Sonesson, R. van Otterdijk, and A. Meybeck, editors. Save Food International Congress. Food and Agriculture Organization of the United Nations, Rome, Italy.

Fedriani, J. M., T. K. Fuller, and R. M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325–331. https://doi.org/10.1111/J.1600-0587.2001.TB00205.X

Ferrera, M. 2016. Aspectos ecológicos del mapache (*Procyon lotor*) y su relación con los turistas en el Parque Nacional Manuel Antonio, Costa Rica. Thesis, Universidad Nacional, Heredia, Costa Rica.

Ficetola, G. F. 2008. Impacts of human activities and predators on the nest success of the hawksbill turtle, *Eretmochelys imbricata*, in the Arabian Gulf. Chelonian Conservation and Biology 7:255–257. https://doi.org/10.2744/CCB-0700.1

Fritzell, E. K. 1978. Reproduction of raccoons (*Procyon lotor*) in North Dakota. American Midland Naturalist 100:253–256. https://www.jstor.org/stable/2424800

Gallo, T., M. Fidino, B. Gerber, A. A. Ahlers, J. L. Angstmann, M. Amaya, A. L. Concilio, D. Drake, D. Gay, E. W. Lehrer, et al. 2022. Mammals adjust diel activity across gradients of urbanization. Elife 11:e74756. https://doi.org/10.7554/eLife.74756

Gandu, M., M. López-Mendilaharsu, D. Goldberg, G. López, and F. Tognin. 2013. Predation of sea turtle nests by armadillos in the northern coast of Bahia, Brazil. Marine Turtle Newsletter 139:12–13. http://www.seaturtle.org/mtn/archives/mtn139/mtn139-4.shtml

Garrott, R. A., P. J. White, and C. A. Vanderbilt-White. 1993. Overabundance: an issue for conservation biologists? Conservation Biology 7:946–949. https://doi.org/10.1046/j.1523-1739.1993.740946.x

Gehrt, S. D. 2004. Ecology and management of striped skunks, raccoons, and coyotes in urban landscapes. Pages 81–104 *in* N. Fascione, A. Delach, and M. E. Smith, editors. People and predators: from conflict to coexistence. Island Press, Washington, D.C., USA.

Gehrt, S. D., W. F. Gergits, and E. K. Fritzell. 2008. Behavioral and genetic aspects of male social groups in raccoons. Journal of Mammalogy 89:1473–1480. https://doi.org/10.1644/07-MAMM-A-403.1

Graser, W. H., S. D. Gehrt, L. L. Hungerford, and C. Anchor. 2012. Variation in demographic patterns and population structure of raccoons across an urban landscape. Journal of Wildlife Management 76:976–986. https://doi.org/10.1002/JWMG.344

Gross, J., F. Elvinger, L. L. Hungerford, and S. D. Gehrt. 2012. Raccoon use of the urban matrix in the Baltimore Metropolitan Area, Maryland. Urban Ecosystems 15:667–682. https://doi.org/10.1007/S11252-011-0218-Z

Hamer, A. J., and M. J. McDonnell. 2010. The response of herpetofauna to urbanization: inferring patterns of persistence from wildlife databases. Austral Ecology 35:568–580. https://doi.org/10.1111/J.1442-9993.2009.02068.X

Hartig, F., L. Lohse, and M. Souza Leite. 2024. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models (version 0.4.7). https://doi.org/10.32614/CRAN.PACKAGE.DHARMA

Heithaus, M. R. 2013. Predators, prey, and the ecological roles of sea turtles. Chapter 10 *in* J. Wyneken, K. J. Lohmann, and J. A. Musik, editors. The biology of sea turtles. 3. CRC Marine Science Series, Boca Raton, Florida, USA.

Honey, M. 2003. Giving a grade to Costa Rica's green tourism. NACLA Report on the Americas 36:39–47. https://doi.org/10.1080/10714839.2003.11724546

Instituto Costarricense de Turismo [ICT]. 2024. 2023 llega a cifra récord de arribo de turistas con 2,47 millones por la vía aérea. Instituto Costarricense de Turismo, San José, Costa Rica. https://www.ict.go.cr/es/noticias-destacadas/2269-2023. Accessed 23 Oct 2024.

Ishiguro, Y. 2023. Morphological studies on the genital organ in the raccoon (*Procyon lotor*). Dissertation, Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Japan.

Larson, R. N., D. J. Morin, I. A. Wierzbowska, and K. R. Crooks. 2015. Food habits of coyotes, gray foxes, and bobcats in a coastal southern California urban landscape. Western North American Naturalist 75:339–347. https://scholarsarchive.byu.edu/wnan/vol75/iss3/10

Leighton, P. A., J. A. Horrocks, and D. L. Kramer. 2011. Predicting nest survival in sea turtles: when and where are eggs most vulnerable to predation? Animal Conservation 14:186–195. https://doi.org/10.1111/J.1469-1795.2010.00422.X

Lenth, R. 2025. emmeans: estimated marginal means, aka least-squares means (R package version 1.11.1-00001). https://github.com/rvlenth/emmeans.

Lesnoff, M., and R. Lancelot. 2022. aods3: analysis of overdispersed data using S3 methods (aods3 package version 0.4-1.2). https://CRAN.R-project.org/package=aods3

Lovemore, T. E. J., N. Montero, S. A. Ceriani, and M. M. P. B. Fuentes. 2020. Assessing the effectiveness of different sea turtle nest protection strategies against coyotes. Journal of Experimental Marine Biology and Ecology 533:151470. https://doi.org/10.1016/J.JEMBE.2020.151470

Lowry, H., A. Lill, and B. B. M. Wong. 2013. Behavioural responses of wildlife to urban environments. Biological Reviews 88:537–549. https://doi.org/10.1111/BRV.12012

Madden, D., J. Ballestero, C. Calvo, R. Carlson, E. Christians, and E. Madden. 2008. Sea turtle nesting as a process influencing a sandy beach ecosystem. Biotropica 40:758–765. https://doi.org/10.1111/J.1744-7429.2008.00435.X

Maxar. 2024. High-resolution Satellite Imagery. https://www.maxar.com/maxar-intelligence/products/satellite-imagery. Accessed 10 Oct 2024.

Mayer, A. E., L. S. Ganoe, C. Brown, and B. D. Gerber. 2023. Diel activity structures the occurrence of a mammal community in a human-dominated landscape. Ecology and Evolution 13(11):10684. https://doi.org/10.1002/ece3.10684

Mcdonald, R. I., P. Kareiva, and R. T. T. Forman. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. Biological Conservation 141:1695–1703. https://doi.org/10.1016/j.biocon.2008.04.025

Méndez-Rodríguez, L., and S. T. Álvarez-Castañeda. 2016. Predation on turtle nests in the southwestern coast of the Baja California Peninsula. Revista Mexicana de Biodiversidad 87:483–488. https://doi.org/10.1016/j.rmb.2016.02.005

Mims, D. M., S. A. Yasuda, and J. J. Mark. 2022. Contrasting activity times between raccoons (*Procyon lotor*) and Virginia opossums (*Didelphis virginiana*) in urban green spaces. Northwestern Naturalist 103:63–75. https://doi.org/10.1898/1051-1733-103.1.63

Montalvo, V. H., C. Saénz-Bolanõs, L. D. Alfaro, J. C. Cruz, F. H. Guimarães-Rodrigues, E. Carrillo, C. Sutherland, and T. K. Fuller. 2019. Seasonal use of waterholes and pathways by macrofauna in the dry forest of Costa Rica. Journal of Tropical Ecology 35:68–73. https://doi.org/10.1017/S0266467418000457

Nix, J. H., R. G. Howell, L. K. Hall, and B. R. McMillan. 2018. The influence of periodic increases of human activity on crepuscular and nocturnal mammals: testing the weekend effect. Behavioural Processes 146:16–21. https://doi.org/10.1016/j.beproc.2017.11.002

Oe, S., M. Sashika, A. Fujimoto, M. Shimozuru, and T. Tsubota. 2020. Predation impacts of invasive raccoons on rare native species. Scientific Reports 10:20860. https://doi.org/10.1038/s41598-020-77016-y

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501–1514. https://doi.org/10.1111/ele.12187

Piedra, R., E. Velez, P. Dutton, E. Possardt, and C. Padilla. 2007. Nesting of the leatherback turtle (*Dermochelys coriacea*) from 1999–2000 through 2003–2004 at Playa Langosta, Parque Nacional Marino Las Baulas de Guanacaste. Chelonian Conservation and Biology 6:111–116. https://doi.org/10.2744/1071-8443(2007)6[111:NOTLTD]2.0.CO;2

Pitt, J. A., S. Larivière, and F. Messier. 2008. Social organization and group formation of raccoons at the edge of their distribution. Journal of Mammalogy 89:646–653. https://doi.org/10.1644/07-MAMM-A-224R.1

Prange, S., and S. D. Gehrt. 2004. Changes in mesopredator-community structure in response to urbanization. Canadian Journal of Zoology 82:1804-1817. https://doi.org/10.1139/z04-179

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. Journal of Wildlife Management 67:324–333. https://doi.org/10.2307/3802774

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. Journal of Mammalogy 85:483–490. https://doi.org/10.1644/1383946

Proctor, T. L., F. Fatungase, J. A. Barquero Leiva, F. J. López-Navas, C. E. Durr, and F. V. Paladino. 2025. Tiny patch, big value: a small dry forest patch supports wildlife conservation in Guanacaste, Costa Rica. Ecology and Evolution 15:e71972. https://doi.org/10.1002/ece3.71972.

Proudman, N. J., and M. L. Allen. 2025. Habitat features, coyotes, and humans drive diel activity variation among sympatric mammals. Integrative Zoology 21:13000. https://doi.org/10.1111/1749-4877.13000

R Core Team. 2023. R: a language and environment for statistical computing. Version 4.1.2. R Foundation for Statistical Computing, Vienna, Austria.

Real, E., D. Oro, A. Martínez-Abraín, J. M. Igual, A. Bertolero, M. Bosch, and G. Tavecchia. 2017. Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. Journal of Avian Biology 48:1462–1470. https://doi.org/10.1111/jav.01454

Rutledge, M. L., F. V. Paladino, J. R. Spotila, and P. Santidrián Tomillo. 2024. Shifting thermal tolerance windows throughout incubation affects sea turtle hatching success: implications for hatchery management and conservation. Marine Biology 172:3. https://doi.org/10.1007/S00227-024-04566-4

Santidrián Tomillo, P., L. Fonseca, F. V. Paladino, J. R. Spotila, and D. Oro. 2017. Are thermal barriers "higher" in deep sea turtle nests? PLOS ONE 12:e0177256. https://doi.org/10.1371/journal.pone.0177256

Santidrián Tomillo, P., F. V. Paladino, J. S. Suss, and J. R. Spotila. 2010. Predation of leatherback turtle hatchlings during the crawl to the water. Chelonian Conservation and Biology 9:18–25. https://doi.org/10.2744/ccb-0789.1

Seminoff, J. A. 2004. *Chelonia mydas*. The IUCN Red List of Threatened Species 2004: e.T4615A11037468. https://doi.org/10.2305/IUCN.UK.2004.RLTS.T4615A11037468.en

Stancyk, S. 1982. Non-human predators of sea turtles and their control. Pages 139–152 *in* K. A. Bjorndal, editor. Biology and conservation of sea turtles. Smithsonian Institution, Washington, D.C., USA. https://cir.nii.ac.jp/crid/1570291225245100160

Troyer, E. M., S. E. Cameron Devitt, M. E. Sunquist, V. R. Goswami, and M. K. Oli. 2014. Survival, recruitment, and population growth rate of an important mesopredator: the northern raccoon. PLOS One 9:e98535. https://doi.org/10.1371/journal.pone.0098535

United Nations. 2018. World urbanization prospects: the 2018 revision. United Nations, Department of Economic and Social Affairs, Population Division, New York, New York, USA.

Vázquez Muñoz, M. 2002. Tourism and conservation in southern Costa Rica. Thesis, York University, Toronto, Canada.

Wallace, B. P., M. Tiwari, and M. Girondot. 2013. *Dermochelys coriacea*. The IUCN Red List of Threatened Species 2013:e.T6494A43526147.

Welicky, R. L., J. Wyneken, and E. G. Noonburg. 2012. A retrospective analysis of sea turtle nest depredation patterns. Journal of Wildlife Management 76:278–284. https://doi.org/10.1002/jwmg.255

Woolard, J., R. M. Engeman, H. T. Smith, and J. Griner. 2004. Cheloniidae (marine turtle) nest predation. USDA National Wildlife Research Center, Washington, D.C., USA.

Wright, J. D., M. S. Burt, and V. L. Jackson. 2012. Influences of an urban environment on home range and body mass of Virginia opossums (*Didelphis virginiana*). Northeastern Naturalist 19:77–86. https://doi.org/10.1656/045.019.0106

Associate Editor: Bill Harrower.

SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

How to cite this article: Cordero-Umaña, K. E., K. Stevens, A. Yaney-Keller, J. López Navas, F. V. Paladino, J. R. Spotila, and P. Santidrián Tomillo. 2026. Indirect effects of fast-growing urban development on wildlife in a coastal protected area of Costa Rica. Journal of Wildlife Management e70174. https://doi.org/10.1002/jwmg.70174