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Insights into the human-jaguar *Panthera onca* (Carnivora: Felidae) interactions in Tortuguero National Park, Costa Rica

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ABSTRACT. Introduction: Human-wildlife interactions are on the rise due to anthropogenic pressures. Understanding these interactions is crucial for preventing conflict and promoting coexistence, ultimately benefitting humans and wildlife. **Objective:** In this study, we analysed the interactions between humans and jaguars *Panthera onca* in Tortuguero National Park, Costa Rica. **Methods:** We examined data concerning jaguar sightings within Tortuguero National Park, Costa Rica compiled from 2000 to 2022. **Results:** A total of 381 jaguar sightings were recorded, of which 75% occurred in the coastal habitat; 81% occurred during the leatherback sea turtle *Dermochelys coriacea* (March-May) and the green sea turtle *Chelonia mydas* (June-October) nesting seasons. From photographic records, 26 individual jaguars were identified (14 females, 12 males). Furthermore, 9% of the sightings were reported within the boundaries of Tortuguero village, where at least 48 domestic dogs *Canis lupus familiaris* were attacked by jaguars. **Conclusions:** Despite the jaguar's cryptic nature, the data show an increase in the frequency and duration of jaguar sightings over the years. This trend is likely due to an increase in the local jaguar population and possibly an increase in jaguars' tolerance towards humans, possibly triggered by people's inappropriate behaviour (e.g. approaching jaguars while feeding, mating or with their cubs) during the sightings. Our study also highlights the potential for conflict due to jaguar predation of domestic dogs, which is increasing within the study area. Therefore, there is a need for management action to promote coexistence between humans and the local jaguar population in Tortuguero National Park, Costa Rica.

Keywords: Coexistence, *Panthera* onca, conflict, sightings, wild cat, *Canis lupus familiaris.*

RESUMEN. "Percepción sobre las interacciones humano-jaguar *Panthera onca* (Carnivora: Felidae) en el Parque Nacional Tortuguero, Costa Rica". **Introducción:** Las interacciones entre los seres humanos y la vida silvestre han aumentado debido a las presiones antropogénicas. Comprender estas interacciones es crucial para prevenir conflictos y fomentar la coexistencia. **Objetivo:** Analizar las interacciones entre los humanos y los jaguares *Panthera onca* en el Parque Nacional Tortuguero, Costa Rica. **Métodos:** Analizamos una base de datos (2000-2022) correspondientes a los avistamientos de jaguares en el Parque Nacional Tortuguero, Costa Rica. **Resultados:** Registramos un total de 381 avistamientos de jaguares, de los cuales el 75% ocurrieron en el hábitat costero, mientras que el 81% durante las temporadas de anidación de la tortuga baula *Dermochelys coriacea* (marzo-mayo) y la tortuga verde *Chelonia mydas* (junio-octubre). A partir de los registros fotográficos, se identificaron 26 jaguares (14 hembras, 12 machos). Además, el 9% de los avistamientos ocurrieron dentro de los límites del pueblo de Tortuguero, donde al menos 48 perros domésticos *Canis lupus familiaris* han sido atacados por jaguares. **Conclusión:** A pesar de la naturaleza críptica del jaguar, los datos muestran un aumento en la frecuencia y duración de los avistamientos a lo largo de los años. Es probable que esta tendencia se deba a un aumento de la población local de jaguares, y posiblemente a un aumento de la tolerancia de los jaguares hacia los humanos provocado probablemente por el comportamiento inadecuado de las personas (por ejemplo, acercarse a los jaguares mientras se alimentan, se aparean o están con sus crías) durante los avistamientos. Nuestro estudio también destaca el potencial de conflicto debido a la depredación de perros domésticos por parte de los jaguares, que está aumentando en el área de estudio. Por lo tanto, es necesaria la toma de decisiones de manejo para promover la coexistencia entre los humanos y la población local de jaguares en el Parque Nacional Tortuguero, Costa Rica.

Palabras clave: Coexistencia, *Panthera onca*, conflicto, avistamientos, felino silvestre, *Canis lupus familiaris.*

Human-wildlife interactions refer to any situation in which people and wild animals come into contact with each other (Gross et al., 2021). The frequency of these interactions has been increasing globally due to the growth of the human population and the expansion of human activities into the natural habitats of wild animals (Gross et al., 2021; Narayan & Rana, 2023). Climate change has also contributed to the rise in interactions (Abrahms et al. 2023). Although these interactions can be positive and not cause distress to either party, they can also have negative outcomes for humans or wildlife, which can lead to human-wildlife conflict (Castaño-Uribe et al., 2016; Nyhus, 2016). Such conflict requires a multidisciplinary approach to achieve coexistence between humans and wildlife (Marchini et al., 2016).

Protected areas play a crucial role in the conservation of jaguars *Panthera onca* as they provide essential resources such as prey, refuge, and water (Quigley et al., 2015). Despite jaguars' tendency to avoid humans, various threats, such as decreased in prey availability and habitat fragmentation, have forced the species to explore new territories beyond protected areas, bringing them closer to human settlements and increasing the chances of human-jaguar interactions (Sanderson et al., 2002; Conde et al., 2010; Foster et al., 2010). Extensive research has been carried out on the interactions between humans and jaguars in the Americas. A recent study by Rubio-Rocha et al. (2023) provides an overview of current knowledge by reviewing publications on the species between 1985 and 2021. The study categorises human-jaguar interactions as direct and indirect. Direct interactions refer to attacks by jaguars on humans and the hunting of the jaguars. Indirect interactions include the impact of human activities on jaguars and human perception towards the species.

In Costa Rica, there have been several studies on human-jaguar interactions (Hilje & Monge, 1988; Corrales-Gutiérrez et al., 2011; Amit et al., 2013; Corrales-Gutiérrez, 2016; Montalvo et al., 2016; Sistema Nacional de Áreas de Conservación [SINAC], 2018; Kelly, 2019; Araya-Gamboa et al., 2024). However, there is limited research available in Tortuguero National Park, Costa Rica. Regarding direct interactions, Arroyo-Arce et al. (2014) and Corrales-Gutiérrez (2016) have reported cases of livestock predation, as well as retaliatory hunting of the species due to conflict in the communities located within the buffer area of the national park. Concerning indirect interactions, some authors studied the impact of habitat features on jaguar occupancy and the perception of local communities towards the felid (Arroyo-Arce, 2013; Arroyo-Arce et al., 2014; Brenes & Coto, 2021). The objective of our study was to gain insight into the interactions between humans and jaguars in Tortuguero National Park, Costa Rica, over a 23-year period.

MATERIALS AND METHODS

Study area: Tortuguero National Park is located on the northeast Caribbean coast of Costa Rica (10°32'28" N - 83°30'08'' W, Fig. 1A & 1B), and encompasses an approximate terrestrial area of 45 755ha. The predominant ecosystem is the Tropical Wet Forest (Holdridge, 1969). Elevation ranges from 0m to 311m above sea level. The average temperature is between 25°C and 30°C, with a mean annual precipitation of 6 000mm (Bermúdez & Hernández, 2004). The national park is bordered to the northwest by the Barra del Colorado Wildlife Refuge and Tortuguero Protected Zone. The Western and Southern edges of the national park are bordered by communities that are economically dependent on crop farming (mainly banana and pineapple), extensive livestock farming (meat and milk), and to a lesser extent, tourism (Ling, 2002; Bermúdez & Hernández, 2004).

Within Tortuguero National Park there is a small village (1 200–1 500 inhabitants) called Tortuguero (Fig. 1B), which can only be accessed by boat or airplane, and whose primary source of income is eco-tourism (SINAC, 2013). The village hosts a large domestic dog *Canis lupus familiaris* population, and while some are well cared for by their owners, others are abandoned or allowed to

roam free or tied by the houses without proper care. These malnourished dogs typically do not receive adequate veterinary care beyond occasional sterilisation and vaccination campaigns as the village does not have a veterinary clinic (Arroyo-Arce pers. obs.). Additionally, they often feed on garbage or roam free in the coastal habitat, preying on sea turtle nests by digging up and eating the eggs and hatchlings (Guerrero et al., 2022).

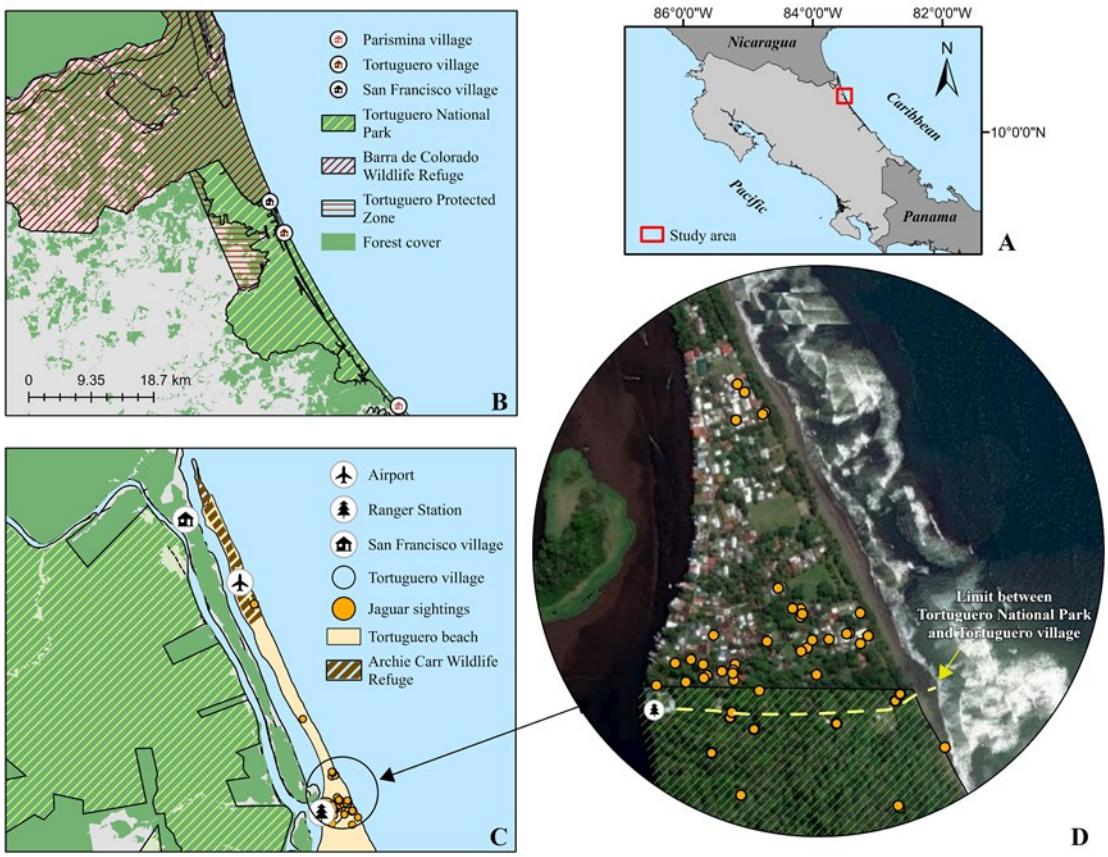

Fig. 1. Location of Tortuguero National Park, Costa Rica (A, B), with details of the spatial distribution of jaguar *Panthera onca* sightings in Tortuguero village (C, D).

Data Collection: Data were collected between 2000 and 2022, in which strict reliability criteria were established. Each jaguar sighting was verified by a primary witness who provided an accurate species description without prompting. Key details for each sighting were recorded, including the date, time, observer name, geographic location, estimated length of the encounter (min), estimated distance between the observer and the jaguar (m), number of observers, number of jaguars observed, the perceived behavioral response of the jaguar towards people during the sightings (Table 1), remarkable observations if any (e.g. jaguar attacks on domestic animals), and photographic evidence if available. To identify individual jaguars, the images were cross-referenced with a photographic database previously established by our project in the study area (I. Thomson unpublished data).

TABLE 1

Classification of the perceived behavioural response of the jaguar *Panthera onca* towards people during a sighting in Tortuguero National Park, Costa Rica

Classification	Definition
Observant	Jaguar notices people and observes them in a non-threatening manner. It does not leave the site.
Defensive	Jaguar shows aggression (e.g. vocalisation, mock attacks) towards people when approached. It either remains or leaves the site.
Inquisitive	Jaguar approaches people in a non-threatening manner when noticing their presence. It does not leave the site.
Avoiding humans	Jaguar walks away or flees the site when noticing people or when approached by people.

RESULTS

Characterization of jaguar sightings: A total of 381 jaguar sightings were recorded in the study area. Over the years, the number of jaguar sightings has increased, with the highest number recorded in 2021 (62 sightings; Fig. 2A). Sighting frequency also fluctuated throughout each year, with the majority of sightings occurring during the leatherback sea turtle *Dermochelys coriacea*, and the green sea turtle *Chelonia mydas* nesting seasons (Fig. 2B). Among the observers, researchers working in the area reported most of the sightings (66%), followed by park rangers (16%), members of the local communities (11%), and tourist guides (7%). Additionally, in 94% of the sightings, the number of observers was recorded, and of those, 91% were groups of less than 5 people (Fig. 3A). Furthermore, the estimated distance between the observer and the jaguar was reported for 58% of the sightings, with 21% of these sightings occurring at less than 10m (Fig. 3B).

Regarding the location, 75% of the sightings occurred in the coastal habitat. In comparison, 10% were reported on the canals (e.g. jaguar swimming or resting on the canal banks), 9% within the boundaries of Tortuguero village, and 6% within the national park forest trails. In 85% of the jaguar sightings, the time of the sighting was reported. Of these sightings, 34% occurred during the diurnal period, 33% during the nocturnal period and 33% during crepuscular times. The length of the sighting was recorded for 54% of the sightings, and 57% of those lasted less than one minute (Fig. 3C). Additionally, 78% of the sightings involved a single jaguar, while 17% featured two jaguars, 4% had three jaguars, and 1% had four jaguars. From 58 sightings with photographic records, we were able to identify 26 individuals, including 14 females and 12 males (Appendix Table 2). The jaguar's behavioural response towards humans during the sightings was recorded for 32% of the events, and in 66% of those the jaguar avoided people (Fig. 3D).

It is worth noting that out of all the observations made, 48 cases were linked to jaguars predating domestic dogs, out of which 14 survived the attack. The first incident was reported in 2016, with three cases in 2017, one in 2019, and the remaining cases between 2020 and 2021. A total of 43 events took place in Tortuguero village and mainly occurred at night (18:00 to 6:00) between November and March. Furthermore, most observations indicate that the attacks occurred when dogs were roaming free, with some cases happening when dogs were tied by the owners' house.

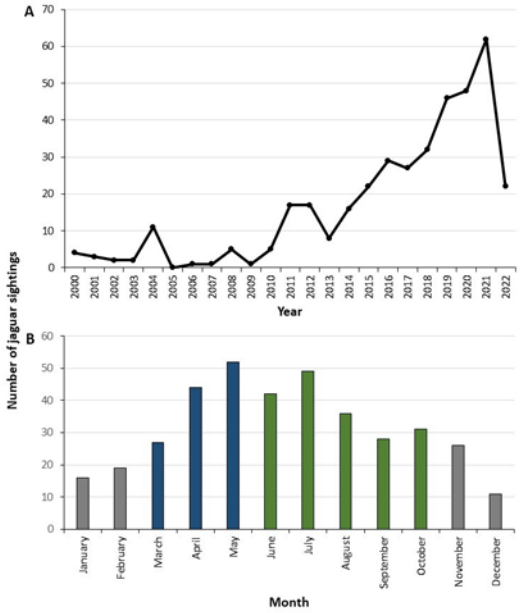

Fig. 2. Jaguar *Panthera onca* sightings recorded in Tortuguero National Park, Costa Rica. (A) annual records, (B) monthly records; grey bars: not sea turtle nesting season; blue bars: leatherback sea turtle *Dermochelys coriacea* nesting season; green bars: green sea turtle *Chelonia mydas* nesting season.

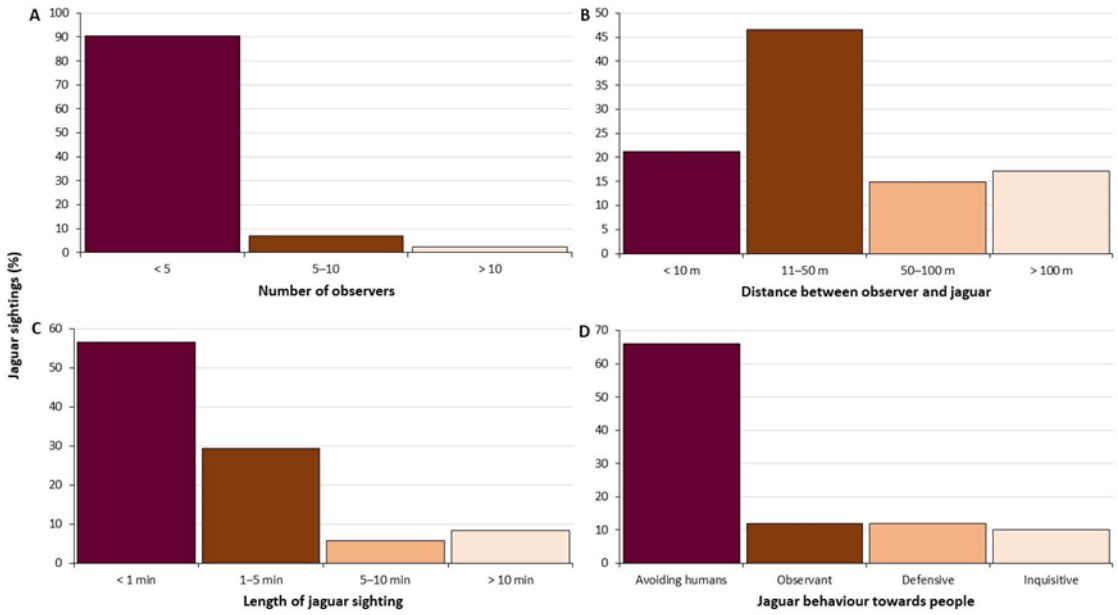

Fig. 3. Characterization of jaguar *Panthera onca* sightings recorded in Tortuguero National Park, Costa Rica during the period 2000-2022. (A) number of observers, (B) distance (m) between the observer and jaguar, (C) length (min) of the sighting, (D) perceived jaguar behaviour during the sightings.

Noteworthy cases of jaguar sightings: On 12 May 2015 at 07:35, a group of five researchers, conducting fieldwork in the coastal habitat, saw four jaguars next to a fresh carcass (< 24h since predation) of a leatherback sea turtle. The carcass had been predated by a jaguar the night before. The researchers called the Research Field Station (located roughly one mile south) about the sighting. Shortly, around 20 volunteers and staff arrived at the site and observed the jaguars from

approximately 30m for almost two hours. During the sighting, one of the jaguars, later identified as an adult female based on the photographic records available, showed observant behaviour (Table 1) towards the people, while the other three jaguars, later identified as her cubs (two males and one female) were feeding from the carcass. The next day, the same group of people returned to the same site at 06:26h where the jaguar family group was again feeding from the carcass. This time they observed the jaguars from roughly 100m for about two hours. The adult female jaguar continued to show observant behaviour towards the presence of people.

Another case worth mentioning was reported on 11 July 2019 at 07:00, two park rangers were on patrol when they spotted three jaguars feeding from a fresh green sea turtle carcass. The jaguars were later identified as an adult female and her two cubs, based on the photographic records available. Despite being aware of the rangers' presence, the jaguars did not leave the site. The cubs played and fed from the carcass, occasionally moving in and out of the vegetation. At one point, the rangers approached the carcass, causing the cubs to run away into the vegetation, but they quickly returned. One of the cubs even sniffed the ranger's shoes. During this entire time, their mother remained nearby (at approximately 20m), initially displaying defensive behaviour towards the rangers but later becoming more observant (even lying down) while her cubs fed from the carcass. This sighting lasted roughly 45 min, after which the jaguar family group left the site.

Other cases to be highlighted are three instances where jaguars followed people for short distances. The first occurred on 21 March 2016 at 21:34 when a group of six researchers conducted a night survey on a trail and encountered a jaguar (later identified as an adult male individual based on the photographic records available) lying in the middle of the trail at 20m distance. The jaguar showed inquisitive behaviour towards the group, rising to follow them in a non-threatening manner for around 16 min as they backtracked along the trail, keeping a 15 to 40m distance. After this, the jaguar walked into the vegetation, and the researchers returned to the field station. The second instance occurred on 5 September 2017 at 20:05, four researchers encountered a jaguar on the trail running parallel to the beach while conducting a night survey. The jaguar followed the group for approximately 75m distance and then moved into the vegetation. Lastly, on 4 July 2021 at 19:45, a group of four researchers encountered two jaguars while walking along a trail. The jaguars were 15m from the group. When the jaguars started following the group, one person tried to scare them away by blowing a whistle, but the jaguars did not react. As a result, the group decided to back up and leave the trail. The whole encounter lasted for approximately 2 min.

Another noteworthy trend is the recent increase in jaguar sightings in Tortuguero village (Fig. 1C & 1D). Although historically the jaguar has been reported sporadically in and around the village (Arroyo-Arce, 2013), since 2019 they have been seen more regularly patrolling the trail that limits the south end of the village with the national park (Fig. 1D). There have even been reports of jaguars venturing into the village, where locals have observed them on sidewalks, and in gardens, and even entering the properties of small hotels and predating dogs. It is important to highlight that there is no physical barrier, like a fence, that could prevent a jaguar from moving between the national park and the village, and that some properties are directly adjacent to the forest. Additionally, most local buildings do not have complete physical barriers that may restrict the jaguar's movements into their properties.

DISCUSSION

Throughout our 23-year monitoring program, we have noticed significant changes in jaguar sighting patterns. While records indicate that jaguars have been spotted in the coastal habitat of Tortuguero National Park since the 1950s (Harrison et al., 2005), they were rarely seen and would quickly flee upon detection, making it challenging to observe them. This behaviour is consistent with the species' solitary and cryptic nature, large home ranges, and low population densities (Sanderson et al., 2002; Silver et al., 2004). However, in recent years, jaguar sightings have become more frequent and prolonged, and involve not just solitary but multiple individuals.

The increase in jaguar sightings appears to be following a similar trend to the increase in jaguar predation on sea turtles reported in Tortuguero National Park between 2005 and 2022 (Arroyo-Arce & Salom-Pérez, 2015; Arroyo-Arce & Thomson, 2023). One possible explanation for the increased predation rate could be the growth in the local jaguar population, which could also account for the rise in sightings (Arroyo-Arce & Salom-Pérez, 2015). The periods with the highest sightings coincided with the nesting season of the leatherback sea turtle from March to May, and the green sea turtle from June to October. During this time, jaguars tend to restrict their movements to the coastal habitat to prey on sea turtles (Arroyo-Arce et al., 2014; Arroyo-Arce & Salom-Pérez, 2015). It is not surprising that most sightings occurred in the coastal habitat, where people such as researchers spend more time. Additionally, the coastal area, being open and devoid of dense vegetation, offers better visibility than the forest habitat, which can obscure an observer's view (Gau et al., 2001).

Based on the available photographic evidence of jaguar sightings and considering that jaguars are known to limit their movement to the coastal habitat during the nesting season (Arroyo-Arce et al., 2014; Arroyo-Arce & Salom-Pérez, 2015), there were multiple sightings from the same individuals over the study period. The evidence also suggests jaguar sightings were from both transient and resident individuals (S. Arroyo-Arce unpublished data). According to Harmsen et al. (2017), a resident is an individual who has been detected in the study area for at least three consecutive years, whereas a transient individual has been detected for less than two years in a row.

Our research suggests that human behaviour during jaguar sightings may have a negative impact on the species and certain individuals may become more tolerant of human presence over time. Tolerance, in this case, refers to the state of an animal that is exposed to disturbance and exhibits observable behaviours (Nisbet, 2000). This tolerance can be observed through reduced flight initiation distance (the distance at which a jaguar will start to move away from an approaching threat such as humans, as described by Ydenberg & Dill (1986)), the continuation of normal activity (such as feeding from a sea turtle carcass) despite proximity to humans, and absence of obvious indicators of fear (such as vocalisation or mock attacks). This increase in tolerance could explain the overall rise in jaguar sightings, including inside Tortuguero village.

The recent increase in dog predation within Tortuguero village has intensified human-jaguar conflict, which can lead to fear and retaliation towards the felid. Although research on jaguar predation on dogs is limited (Carral-García et al., 2021), there are records of infectious diseases that dogs can transmit to jaguars, such as canine distemper virus, canine parvovirus, and rabies (Nava et al., 2008; Furtado et al., 2013; Onuma et al., 2016). Therefore, the increase in jaguar predation on dogs in Tortuguero village could increase the risk of disease transmission, thus posing a threat to the health of the local jaguar population. It is important to note that jaguar predation on dogs is much larger than is reflected in the data, as many incidents go unreported. This problem is not limited to Tortuguero village alone, as other coastal villages around Tortuguero National Park, including San Francisco and Parismina, have also been affected (Arroyo-Arce pers. obs.).

The occurrence of jaguar sightings and dog predation in Tortuguero village could be

influenced by seasonality, as most events are reported outside the sea turtle nesting season (November to March). Although there is a resident population of jaguars in the coastal habitat, other jaguars from different sectors of Tortuguero National Park and surrounding areas move to the coastal habitat during the sea turtle nesting season (Arroyo-Arce & Salom-Pérez, 2015). The decrease in easy prey normally found during the sea turtle nesting season, and the dispersal of jaguars from the coastal habitat to other areas outside the nesting season, are likely explanations for the seasonality in dog predation. A similar situation was reported by Carral-García et al. (2021) in a coastal village in the Mexican Caribbean, which shares many similarities (socio-economic, pet ownership) with Tortuguero village.

Jaguars tend to avoid humans in their natural habitat and therefore pose little threat (Hoogesteijn et al., 2016). However, there have been a few reports of jaguar attacks on people in South America, specifically in Colombia, Venezuela, Brazil, and Guyana (Neto et al., 2011; Iserson & Francis, 2015; Hoogesteijn et al., 2016; Neto & Haddad, 2019; Haddad et al., 2022; Bombieri et al., 2023; Surjan et al., 2023). Although there are isolated incidents of unprovoked attacks due to the predatory nature of the felid (Neto et al., 2011; Iserson & Francis, 2015), most attacks are provoked by the inappropriate behaviour of people during jaguar sightings (Neto et al., 2011; Hoogesteijn et al., 2016; Neto & Haddad, 2019, Haddad et al., 2022). In such instances, the jaguar attacks not with the intention of predation, but to scare off the perceived threat posed by human behaviour (Neto & Haddad, 2019). Although jaguar temperaments can vary depending on the individual (Hoogesteijn et al., 2016), in general, jaguars tend to be more sensitive in certain situations, such as females with cubs, individuals with freshly killed prey (e.g. sea turtle carcasses), and males with females in heat (Hoogesteijn et al., 2016; Neto & Haddad, 2019; Haddad et al., 2022).

Based on the above and considering that Tortuguero National Park constitutes an important feeding and breeding area for jaguars (Arroyo-Arce & Thomson, 2019), combined with the inappropriate behaviour of people (e.g. approaching jaguars while feeding, mating or with their cubs) recorded during the sightings, the increase in tolerance of certain jaguar individuals towards humans, and the rise in sightings at Tortuguero village, we conclude that the chance of a provoked attack has become more likely. Management actions are required to avoid the possibility of an attack, which could have serious consequences for humans (e.g. death, injuries) and jaguars (e.g. retaliation), making coexistence challenging. It is important to highlight that the records of jaguars following people are not considered an attempt to attack, since no sign of aggression was recorded, but a defence mechanism because most likely the jaguar was following the people for a short distance to get them out of their territory (most likely a juvenile jaguar) or protect a fresh kill (e.g. sea turtle carcass). Occurrences of jaguars following people are extraordinarily rare, with just some anecdotal records from South America (R. Hoogesteijn pers. obs.; Arroyo-Arce & Thomson, 2019).

Our research has shown a need for local management actions to promote the peaceful coexistence between people and jaguars. As a result of our findings, the administration of Tortuguero National Park (ACTo - Tortuguero Conservation Area) has taken some measures, including prohibiting tourists from entering the southern area of the park (Resolución SINAC-ACTo-D-RES-017-2017) and introducing a code of conduct in the event of a jaguar sighting (Arroyo-Arce & Thomson 2019) for everyone who visits the national park (Resolución SINACACTo-D-RES-053-2016), including park rangers, researchers, tourists, and the local community. Additionally, in collaboration with key stakeholders (e.g. local communities, NGOs, ACTo), we conducted several educational activities (e.g. “The Jaguar is my Neighbour” campaign) to raise awareness among all stakeholders. The purpose of these actions is to reduce human interference with the species and their habitat, to address concerns and perceptions of risk (e.g. jaguar attacks on people), to promote pet welfare (e.g. recommendations on how to protect pets against jaguar attacks), and ultimately, to encourage coexistence between humans and jaguars.

Nonetheless, further efforts are still required to prevent a negative outcome from these interactions. In this regard, even though Tortuguero National Park is the first in Costa Rica to incorporate a code of conduct in the event of a jaguar sighting in its legislation, enforcement is crucial as there are still numerous instances where it is not adhered to by locals, tourists, researchers, and even park rangers. In terms of jaguar predation on dogs, we recommend the following actions: 1) establishing an annual dog census; 2) initiating systematic data collection on dog predation; 3) conducting regular campaigns to promote pet welfare (e.g. sterilisation, vaccination, and health checks); 4) enforcing Costa Rica's Animal Welfare Law (Ley 18298) to ensure responsible pet ownership; and 5) continuing to provide educational activities regarding coexistence. All these actions should target the villages adjacent to the national park, including Tortuguero, San Francisco and Parismina. The issue of jaguars venturing into Tortuguero village can be addressed by installing a non-lethal barrier along the boundary between the village and the national park (Fig. 1D). The barrier could consist of an electric fence along the trail section and wooden posts on the beach section, incorporating both visual and auditory deterrents. This method could prevent jaguars from entering the village and stop free-roaming dogs from entering the national park while allowing other local wildlife to move freely. Although a detailed proposal was submitted to the administration of Tortuguero National Park (ACTo - Tortuguero Conservation Area) at the beginning of 2022 (Arroyo-Arce et al., 2021), to our knowledge, it has not been approved to date. It is important to highlight that similar methods have proven effective deterrents to jaguars across the Americas (Cavalcanti et al., 2012; Quigley et al., 2015).

In conclusion, achieving coexistence between the villages surrounding Tortuguero National Park and the local jaguar population requires specific and customized actions. These actions should be implemented in the short term to prevent the problem from escalating further. If these measures are put in place, Tortuguero National Park could serve as an example of coexistence between humans and wildlife at a national and regional level.

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ETHICAL, CONFLICT OF INTEREST AND FINANCIAL STATEMENTS

The authors declare that they have fully complied with all pertinent ethical and legal requirements, both during the study and in the production of the manuscript; that there are no conflicts of interest of any kind; that all financial sources are fully and clearly stated in the acknowledgements section; and that they fully agree with the final edited version of the article. A signed document has been filed in the journal archives. All co-authors contributed to the study design, data collection, analysis, preparation and final approval of the manuscript.

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APPENDIX

TABLE 2

Jaguar *Panthera onca* individuals identified from photographic records available of sightings in Tortuguero National Park, Costa Rica

Individual	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	Notes
M-01	2	2	1										1 w/F-05* (2011); 1 w/NI (2012); 1 w/F-09* (2013)
M-02	4	1											1 w/F-03* (2011)
F-03	1												1 W/M-02* (2011)
M-04	2												
F-05	2				1				1	1			1 w/M-01* (2011); 1 w/M-15, F-16, M-17** (2015); 1 w/M-25** (2017); 1 w/NI (2020)
M-06	1		1	1									1 w/F-09* (2013)
F-07		2	1		1		1	2		1			1 w/M-08* (2012); 1 w/M-20** (2015); 3 w/NI (2017, 2018, 2020)
M-08		1											1 w/F-07* (2012)
F-09			2										1 w/M-01* (2013); 1 w/M-06* (2013)
F-10			1										
F-11				1		1							1 W/F-12** (2014)
F-12				1									1 w/F-11** (2014)
F-13				1					1				
M-14				2									
M-15					2	1							1 w/F05, F16, M-17**(2015); 1 w/M-17*** (2015)
F-16					1								1 w/F-05, M-15, M-17** (2015)
M-17					3								1 w/F-05, M-15, F-16** (2015); 1 w/M-15*** (2015)
M-18					1	2							
F-19					1								
M-20					1								1 w/F-07** (2015)
F-21						2		1					
F-22							5		1		1	1	
M-23								2	1	1			
F-24									1				1 W/NI (2019)
M-25									1				1 w/F-05** (2017)
F-26											1		
Total	**12**	**7**	**6**	**6**	**11**	**6**	**7**	**6**	**7**	**5**	**2**	**1**	

*Degree of kinship unknown; **Mother-cub; ***Siblings; w/: with; NI: individual not identified