VERTEBRATE BIOLOGY

REVISTA DE Biología Tropical

https://doi.org/10.15517/m5j8t121

Top predator feces: behavioral consequences for coexisting species

Danelly Solalinde[1]; https://orcid.org/0009-0004-0578-6759
Cuauhtémoc Chávez[2*]; https://orcid.org/0000-0003-2201-4748
Gerardo Ceballos[1]; https://orcid.org/0000-0001-8374-2656
Francisco Palomares[3]; https://orcid.org/0000-0002-4655-7205

1. Wildlife Ecology and Conservation Department, Ecology Institute, National Autonomous University of Mexico, Mexico City, Mexico; ddsolalinde@gmail.com, gceballo@ecologia.unam.mx
2. Environmental Sciences Department, Metropolitan Autonomous University, Mexico State, Mexico; j.chavez@correo.ler.uam.mx (*Correspondence)
3. Biology Conservation Department, Doñana Biological Station, CSIC, Seville, Spain; ffpaloma@ebd.csic.es

Received 18-XI-2024. Corrected 11-III-2025. Accepted 18-IX-2025.

ABSTRACT

Introduction: Deposition of feces in the environment is a key behavior in the ecology of predator carnivores, which promotes behavioral changes in animals, influencing the ecology, abundance, and distribution of the species with which they coexist.

Objective: To analyze whether jaguar feces are detected by other jaguars and mammal species and if they have behavioral effects.

Methods: We recorded the behavior of jaguar (*Panthera onca*), puma (*Puma concolor*), mesocarnivores (*Leopardus pardalis*, *Leopardus wiedii*, *Herpailurus yagouaroundi*), and prey species using camera traps, at marked sites (with jaguar feces; n = 28) and control sites (without jaguar feces; n = 10). Using the records, we analyzed, for rainy and dry seasons: (1) the detection of jaguar feces by animals and (2) whether animals modify their exploration, remarking, vigilance and foraging behavior after detecting jaguar feces.

Results: The detection of jaguar feces by jaguars and pumas was similar and the detection was higher in dry season. Regarding the behaviors analyzed, jaguars explored 15 times more and remarked 13 more times, marked sites than control sites. Pumas explored eight times more marked sites than control sites. Mesocarnivores explored marked sites 17 times more than control sites. Prey explored 41 times more and increased their vigilance 24 times more at marked sites compared to control sites times.

Conclusions: Jaguar feces are detected by conspecifics and other mammal species, and they have behavioral effects on them. This can trigger changes in the abundance and distribution of populations and may be one of the ways that large predators shape ecosystems.

Keywords: scent marks; feces detection; animal behavior; top carnivores.

RESUMEN

Heces de depredadores tope: consecuencias conductuales para la coexistencia de las especies

Introducción: La deposición de excremento en el ambiente es un comportamiento clave en la ecología de los carnívoros depredadores, que promueve cambios conductuales en los animales, influyendo en la abundancia y distribución de las especies con las que coexisten.

Revista de Biología Tropical, ISSN: 2215-2075 Vol. 73: e2025-702, enero-diciembre 2025 (Publicado Set. 30, 2025)

Objetivo: Analizar si el excremento de jaguar es detectado por sus conespecíficos y otros mamíferos, y si tiene efectos en el comportamiento de estos.

Métodos: Registramos la conducta del jaguar (*Panthera onca*), puma (*Puma concolor*), mesocarnívoros (*Leopardus pardalis*, *Leopardus wiedii, Herpailurus yagouaroundi*) y presas, mediante cámaras trampa, en sitios marcados (con excremento de jaguar; n = 28) y sitios control (sin excremento de jaguar; n = 10). Con los registros analizamos, para lluvias y secas: (1) la detección de los excrementos de jaguar por animales y, (2) si después de detectar los excrementos de jaguar, los animales modifican su comportamiento de exploración, observación, vigilancia y forrajeo.

Resultados: Pumas y jaguares detectan el excremento con la misma frecuencia y la detección es mayor en temporada seca. En cuanto a las conductas analizadas, los jaguares exploraron 15 veces más y remarcaron 13 veces más, los sitios marcados que los sitios control. Los pumas exploraron ocho veces más los sitios marcados que los sitios control. Los mesocarnívoros exploraron los sitios marcados 17 veces más que los sitios control. Las presas exploraron 41 veces más y aumentaron su vigilancia 24 veces en los sitios marcados que en los sitios de control.

Conclusiones: El excremento del jaguar es detectado por conespecíficos y otras especies de mamíferos y tiene efectos en su conducta. Esto puede desencadenar cambios en la abundancia y distribución de las poblaciones y puede ser una forma en que los carnívoros depredadores moldean los ecosistemas.

Palabras clave: marcas olfativas; detección de heces; conducta animal; carnívoros grandes.

INTRODUCTION

Top carnivores influence the behavior of animals, and it affects the ecology, abundance, and distribution of the species with which they coexist (Epperly et al., 2021; Hoeks et al., 2020; Srivathsa et al., 2023; Wooldridge et al., 2019). One of the most frequent ways carnivores modify animal behavior is through their scent marks, be such as urine, feces, and/or glandular secretions (Allen, Gunther & Wilmers, 2017; Rafiq et al., 2020; Sunde et al., 2022). Carnivores deposit their scent marks in the environment, and the presence of these marks has the potential to modify animal behavior, including conspecifics and other species (Cornhill &Kerley, 2020; Edwards et al., 2022). The scent marks of carnivores primarily have intraspecific functions, such as searching for and selecting a reproductive partner, and defending territories (Miaretsoa et al., 2022; Morehouse et al., 2021). But when the scent marks of top predators are detected by other mammal species, changes or adjustments in the behavior of these animals are activated; which can affect from populations to the functioning of ecosystems (Rafiq et al., 2020; Sunde et al., 2022).

Scent marks are involved and play a determining role in the carnivore ecology. Top carnivores are characterized by being solitary species, having large territories and tending to avoid each other most of the time. In this context, indirect communication between conspecifics mediated by scent marks is convenient (Elbroch & Quigley, 2017; Wooldridge et al., 2019). Scent marks contain information about identity, sex, health, age, and dominance status, and their deposition in the environment is strategic. Carnivore species deposit their scent marks in spatio-temporal patterns that maximize the transmission of the information contained in the marks and increase the probability of being found by other individuals (Allen, Gunther & Wilmers, 2017).

Deposition of scent marks is a behavior involved in the entire carnivore ecology and often has effects on other species (Allen et al., 2023; Hansen et al., 2024). Scent marks of top predators have profound consequences for co-predators and mesocarnivores (Prugh & Sivy, 2020). Subordinate carnivore species can detect the predator presence through their scent marks; when it occurs, avoidance behavior is activated to reduce intraguild predation (Samuel et al., 2020; Sheriff et al., 2020). Avoidance behavior is associated with changes that promote spatial, temporal, and dietary niche segregation (Kemna et al., 2020; Russell et al., 2009; Wooldridge et al., 2019).

Co-predators, mesocarnivores and prey show specific adaptations that allow them to detect predators through scent marks and activate behavioral changes that enable animals to evade predators. Avoidance behavior involves restricting activities at safer areas where top predator scent marks are absent or scarce; generally, these areas are suboptimal sites, and it is more difficult for animals to satisfy their needs (Apfelbach et al., 2005; Sheriff et al., 2020). This compromises the animal fitness and consequently, their abundance, distribution, and ecological functions can be affected (Allen et al., 2024; Wang et al., 2020).

Detecting predator scent marks is essential for the survival, reproduction and fitness of animals so they invest time and energy in detection (Allen et al., 2024; Tallian et al., 2021). Invest in detecting scent marks of predators is positively associated with the risk of predation; when the risk of being predated is higher, the scent marks detection and the time of scent marks exploration increases. In environments with contrasting seasonality, the risk of predation is higher in the dry season than rainy season, so in dry season the detection of scent marks predator by potential prey increases (Herman & Valone, 2000).

Top predator interactions influence the abundance and distribution of species, as well as the structure and functioning of ecosystems (Estes et al., 2011; Lu et al., 2023; Sommers & Chesson, 2019). Frequently, their interactions are based on scent marks that have the potential to modify the behavior of other species: co-predators, mesocarnivores and prey. Consequently, the effects of scent marks on animal behavior are considered a way through which top predators affect the abundance and distribution of the species with which they coexist (Ripple et al., 2014; van Beeck Calkoen et al., 2021). However, the mechanism by which scent marks modify animal behavior has been studied little. This may be due to the difficulty of studying large carnivore predators, which tend to have extensive spatial requirements and be evasive animals, as well as the complexity of recording and analyzing animal behavior in wildlife (Allen, Allen et al., 2017; Allen, Gunther & Wilmers, 2017; Ford, 2017).

The jaguar (*Panthera onca*) is the largest feline and the top predator of the Neotropics; the most frequent route of intraspecific and interspecific interactions is the use of scent marks (Ceballos et al., 2016; Medellín et al., 2016; Palomares et al., 2018). Despite the relevance of scent marks in the ecology of this carnivore, the behavioral effects of scent marks on the behavior of species and their potential implications have been little explored. We analyzed whether jaguar feces are detected by conspecifics, co-predators, mesocarnivores, and prey and the potential behavioral effect on them.

Our hypothesis is that mammals can detect the presence of predators though scents marks and respond by modifying their behavior. Seasonality influences this interaction, with detection frequency varying between dry and rainy seasons. We predict that: 1) jaguar conspecifics, co-predators, mesocarnivores, and prey species will detect jaguar feces; 2) detection frequency will be higher during the dry season compared to the rainy season; 3) animals will modify their behavior in response to detecting jaguar feces. The behavioral changes depend on their interaction with this carnivore. If jaguar conspecifics detect jaguar scent marks, we predict that they increase exploration of feces and show remarking behavior as part of their communication behavior. If the jaguar scent marks are detected by individuals of puma (*Puma concolor*), a co-predator, competitor, and subordinated species, or by individuals of mesopredators, that are also subordinated species with risk of intraguild predation, we predict only an increase in exploration behavior and no remarking behavior. Finally, if any prey species detects jaguar scent marks, we predict an increase in exploration and vigilance behaviors, and a reduction in foraging behavior.

Revista de Biología Tropical, ISSN: 2215-2075 Vol. 73: e2025-702, enero-diciembre 2025 (Publicado Set. 30, 2025)

MATERIALS AND METHODS

Study area: The study area covers 90 Km^2 and includes the Ecological Reserve "El Zapotal" and adjacent areas located in the Northeastern part of the Yucatan Peninsula, Mexico (Fig. 1). El Zapotal is a private reserve acquired for conservation purposes and managed by a non-governmental organization (PRONATURA). The extreme coordinates of the study area are: upper right point 21°22'55" N & 87°31'59" W and lower left point 21°16'52.73" N & 87°36'48.823" W. The bioclimatic system is dry forest (Holddridge, 1967). The climate is tropical sub-humid with an annual average temperature of 25.8 to 26.3 °C and a marked seasonality, rainy season from June to November and dry season for the year, from December to May (Köppen, 1900).

Feces collection: The search for feces was conducted by slowly walking (2-3 km/hr) along all the trails in the study area (a trail system that total 142 km), twice in each season, with a time interval of 60 days. Feces were searched through trails because that is where jaguars and other carnivores frequently deposit them (Palomares et al., 2018). Each feces found was georeferenced and for genetic analysis, a small sample (less than 20 % of the scat) was collected using latex gloves.

Sample genetic identification: Feces samples were preserved in silica gel until their

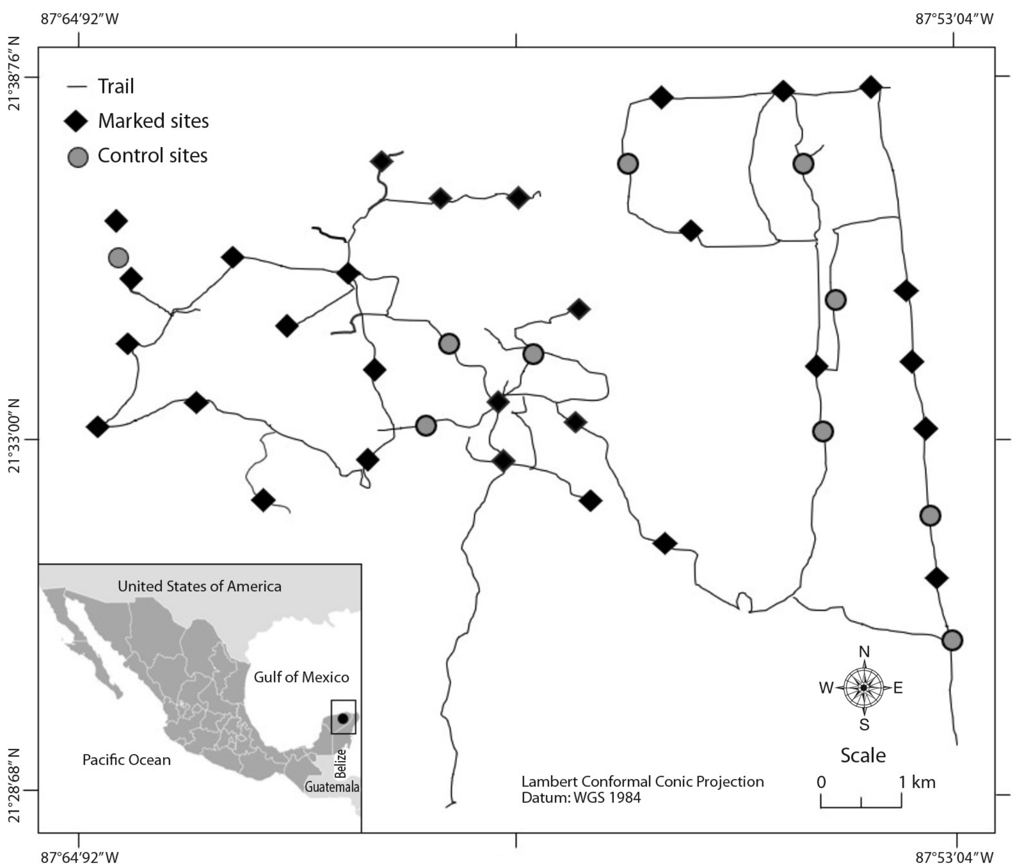

Fig. 1. Study area, in Northern Yucatan Peninsula, Mexico and location of marked (n = 28) and control (n = 10) monitoring sites through trail system.

analysis in the laboratory. DNA was extracted using protocols based on the GuSCN/silica method (Frantz et al., 2003). Each sample was genetically identified at the species level using previously developed species-specific primers, following the method described by Roques et al. (2011). The feces were analyzed to determine sex using the technique described by Pilgrim et al. (2005). Microsatellite markers were used for individual genotyping, as described in Roques et al. (2011). Molecular analysis was undertaken in the Molecular Ecology Laboratory of de Doñana Biological Station (LEM-EBD).

Experimental design: Animal behavior was recorded using camera traps placed at two types of monitoring stations: (1) marked sites by jaguar or sites with jaguar feces (n = 28). We identified these sites during the search for feces along the trails, based on our experience in identifying tracks, and subsequently we genetically confirmed that the feces belonged to jaguar (Roques et al., 2011). The minimum distance between marked sites was one kilometer, and (2) Control sites or unmarked sites (without jaguar feces or n = 10). The criteria for determining these sites were the absence of feces within a one-kilometer radius (Fig. 1).

We installed one camera trap (Cuddeback 1 279 model, 20 MP with Infrared Flash for night detection) per monitoring station. At the marked sites, we focus the cameras on the feces to observe in detail the behavior of the animals when they detect it. Cameras traps were programmed to obtain a 30-second video at detection; for 25 days following the initial feces search. Based on the videos obtained and considering independent records (with a minimum interval of one hour or when different individuals were recorded), animal behavior was analyzed.

Data analysis: We analyzed whether jaguar feces are detected by: congeners (jaguar; *Panthera onca*); competitor species: puma (*Puma concolor*); mesocarnivores: ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii*) and jaguarundi (*Herpailurus yagouaroundi*); and prey: eight mammal species were considered as prey, these species represents 83 to 95 % of jaguar diet in similar sites and close to the study area: central american red brocket (*Mazama temama*), white-tailed deer (*Odocoileus virginianus*), white-nosed coati (*Nasua narica*), lowland paca (*Cuniculus paca*), collared peccary (*Tayassu tajacu*), nine-banded armadillo (*Dasypus novemcinctus*), gray fox (*Urocyon cinereoargenteus*), central american agouti (*Dasyprocta punctata*; Ávila-Najera et al., 2018).

Feces detection: To determine whether animals detect jaguar feces, we reviewed videos from camera traps placed at marked sites, for both seasons. We calculated the average number of jaguar feces detection events per day for each animal group. That is, we divided the total number of feces detection events in each camera trap during the sampling period by the number of sampling days (n = 25). We considered as detection event the direct sniffing of feces or approximately one meter away, in both cases we considered that the sniffing should last ≤ 5 seconds.

We analyzed for each animal group whether the average number of jaguar feces detection events per day changes between seasons using t-student test with independent samples.

Behavioral responses: To determine whether animals modify their behavior after detecting jaguar feces, we reviewed the videos from each camera trap placed at marked sites by jaguars and unmarked sites. For each group of animals, in both seasons, we determined the number of events of four behaviors. (1) Exploration: any site investigation activity > 5 seconds, without surveillance status, with or without movement (Murphy, 1978), (2) remarking: the activity of depositing feces, urine or glandular secretions, forming scratches or scratching surfaces, rubbing some part of the body or rolling (Allen et al., 2016), (3) vigilance: when animals carefully observed the environment in an alert state (Houtman, 2003; Kimbrell et al., 2007) and (4) foraging: when feed consumption was observed (Creel et al., 2014; Spalinger & Hobbs, 1992).

We calculated, for each group of animals, the average number of occurrences of each behavior per day; for this, we divided the total number of occurrences of each behavior in each camera trap during the sampling period by the number of sampling days (n = 25). We analyzed each animal group if the average number of occurrences of each behavior per day is different between marked and unmarked sites using t-student test with independent samples. All statistical analysis were fitted with RStudio 4.4.2 program.

RESULTS

We found a total of 93 feces, 80 % belong to jaguars, 5 % were margay or ocelot, 2 % were puma and 13 % could not be identified. We found 1.3 times more jaguar feces in dry season than in rainy season (42 and 32 feces respectively). The jaguar feces belong to five male individuals, which deposited their feces during both seasons.

Feces detection: Jaguar and puma detected jaguar feces with similar frequency ($t_{jaguar\text{-}puma\text{-}detection}$ = -2.0, d.f. = 17, p = 0.05). Moreover, both felines significantly increased their detection frequency of feces in dry season compared to rainy season ($t_{jaguar\text{-}season\ detection}$ = - 2.2, d.f. = 19.1 p < 0.05; $t_{puma\text{-}season\ detection}$ = - 2.1, d.f. = 17, p < 0.05; Fig. 2).

Behavioral responses: For jaguars, the recorded behaviors were exploration and remarking, both behaviors were observed only at marked sites. The frequency of exploration and remarking behaviors of jaguars is different significantly between marked and unmarked sites (Student's t test: $t_{jaguar\text{-}exploration}$ = 2.7, d.f. = 26, p < 0.01; $t_{jaguar\text{-}remarking}$ = 3.1, d.f. = 26, p < 0.01; respectively; Fig. 3). For puma, exploration behavior was significantly higher in marked sites than in unmarked sites (Student's t test: $t_{puma\text{-}exploration}$ = 2.9, d.f. = 8, p < 0.01;

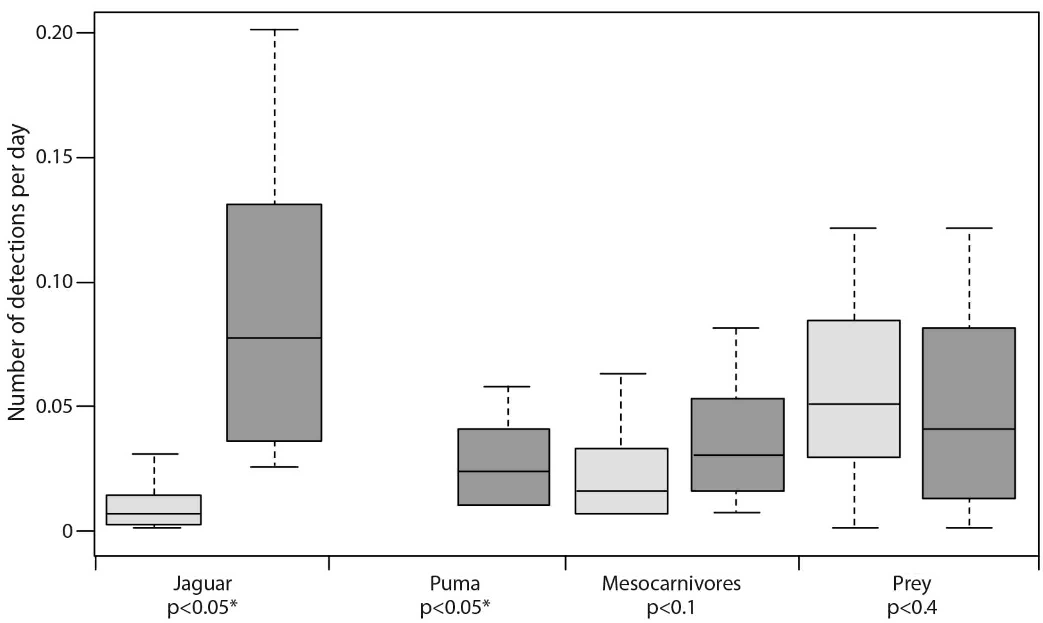

Fig. 2. Number of detections of jaguar feces by group of mammals per day. Light gray = rainy season and dark gray = dry season. Median; Quartiles; Maximum–Minimum.

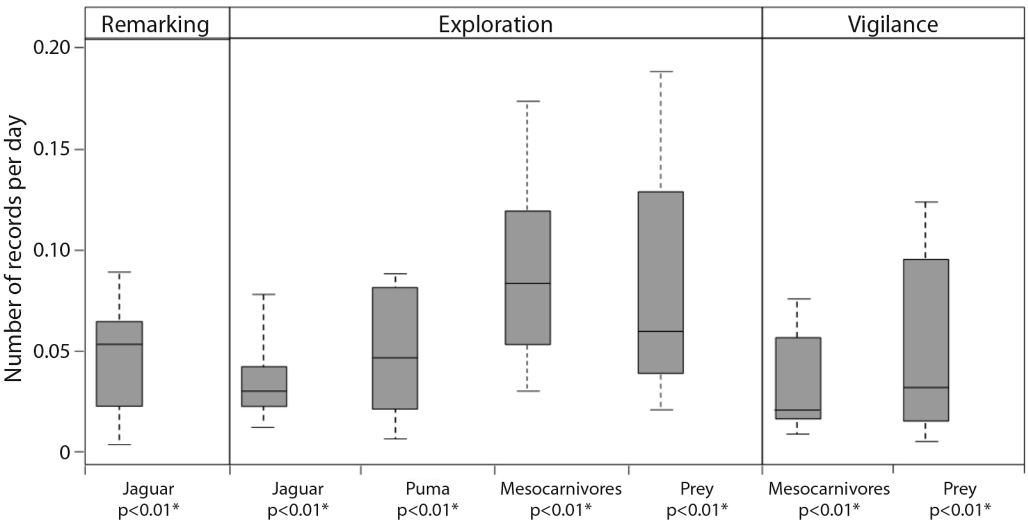

Fig. 3. Behaviors recorded per day in marked (dark grey) and unmarked (light grey) sites by jaguars. Median; Quartile; Maximum–Minimum.

Fig. 3); while remarking behavior does not differ between sites (Student's t test: $t_{\text{puma-remarking}} = 1$, d.f. = 8, p = 0.3; Fig. 3).

For mesocarnivores, the only behavior detected was exploration and its frequency was significantly higher in marked sites by jaguars than in unmarked sites (Student's t-test: $t_{mesocarnivores\text{-}exploration} = 2.6$, df = 20.9, $p < 0.01$; Fig. 3). Prey species significantly increased their exploration and vigilance behaviors in marked sites by jaguars compared to unmarked sites (Student's t-test; $t_{prey\text{-}exploration} = 3.8$, df = 26, $p < 0.01$; $t_{prey\text{-}vigilance} = 4.2$, df = 26, $p < 0.01$, respectively; Fig. 3). In contrast, prey foraging behavior had similar frequency in both sites (Student's t test; $t_{prey\text{-}foraging} = 1.3$, df = 4.3, p = 0.2; Fig. 3).

DISCUSSION

We found that all jaguar feces belonged to male individuals, and that one to four individuals deposit their feces in the same site. This could be related to the defense of territories through scent marks, which is a typical behavior of male carnivores; although this, as in others researches, opens the question of where carnivore females deposit their feces (Allen et al., 2015; Palomares et al., 2018). The deposition of scent marks in common sites, in some carnivore species to facilitate communication between individuals and these sites are often located on the boundaries of territories to reduce intraspecific competition (Buesching & Jordan, 2022; Smith et al., 1989).

Indirectly, the deposition of scents marks in common places promotes spatial and temporal segregation of individuals, which has effects on abundance and distribution of lower trophic levels species (Allen et al., 2015; Allen, Gunther & Wilmers, 2017; Estes et al., 2011). It has been observed in carnivore species such as pumas (*Puma concolor*), cheetahs (*Acinonyx jubatus*) and European badgers (*Meles meles*) (Allen et al., 2015; Buesching & Jordan, 2022; Cornhill & Kerley, 2020). Our results suggest that jaguar deposit feces strategically to reduce competition with neighbors. As a predator, this behavior involves profound ecological effects and to understand them properly it is necessary to study these topics carefully at different scales (Allen et al., 2016; Cornhill & Kerley, 2020).

We observed that (1) jaguar feces are detected by jaguars, pumas, mesocarnivores

Revista de Biología Tropical, ISSN: 2215-2075 Vol. 73: e2025-702, enero-diciembre 2025 (Publicado Set. 30, 2025)

and prey; (2) animals modify their behavior after detecting jaguar feces. Pumas, a co-predator species, detected jaguar feces and explored them with similar frequency to jaguars, but we observed that remarking behavior was different between both carnivores. Remarking behavior was exclusive to jaguars; we did not record remarking behavior in pumas. The behavior observed in pumas, when they detected jaguar feces is consistent with what has been reported in others researches about the dominance of jaguar over puma (Elbroch & Kusler, 2018; Harmsen et al., 2009).

Scent marks are useful for co-predator species to avoid encounters with dominant species and reduce the risk of physical confrontations. Avoiding dominant species promotes niche segregation (spatial, temporal and dietary), which is a fundamental mechanism for coexistence of species with similar ecology (Karanth et al., 2017 Kemna et al., 2020; Müller et al., 2022; Palomares et al., 2016). We observed that puma detects and explores jaguar feces; according to the theory, jaguar feces could allow pumas to recognize the spatiotemporal presence of the jaguar, triggering avoidance behaviors. In this context feces could be considered as an element that promotes the segregation of these large felines and facilitates their coexistence.

Intraguild competition has a strong impact on population dynamics and ecosystem structure (Bai et al., 2021; Davis et al., 2021). Top predators are responsible for one third of mesocarnivores mortality, and to avoid top predators, mesocarnivores have developed avoidance behaviors that are activated when they detect predation risk (Allen et al., 2024; Prugh & Sivy, 2020). Predator scent marks are interpreted by mesocarnivores as signals of predation risk, allowing them to detect and recognize the presence of top predators (Prugh & Sivy, 2020). Upon finding scent marks of predators, mesocarnivores modify their behavior to avoid predators, including changes in activity patterns, spatial movements, home ranges, foraging behavior and even diet composition. (Haswell et al., 2018). These behavioral changes reduce the risk of predation but imply negative effects on their survival and reproduction chances, reducing fitness (Ruprecht et al., 2021; Sheriff et al., 2020).

We observed that mesocarnivores (*L. pardalis*, *L. wiedii*, *H. yagouaroundi*) detected and explored jaguar feces, which suggests that they could detect and recognize the jaguar presence through their feces, as predicted by theory. However, after feces detection, we did not observe changes in their vigilance and foraging behavior. Nevertheless, it is expected that changes will occur in behaviors that we did not evaluate or even some components of vigilance and foraging behavior that were not the focus of this study. Further research is needed to understand the effect of jaguar feces on the behavior and fitness of mesocarnivores. Studying behavioral responses of mesocarnivores to avoid predation and its consequences is crucial and the first step to understand the importance of intraguild predation in ecosystem functioning (Haswell et al., 2018).

Prey detected jaguar feces, and it is very likely that prey perceives it as an indicator of predation risk, as prey increased their exploration and vigilance in marked sites by jaguars. Increase exploration and vigilance behavior helps prey avoid predation but also leads to changes in animal ecology, such as spatiotemporal movements, habitat use, animal nutrition or reproduction rates, which frequently have negative effects on animal fitness (Altendorf et al., 2001; Laundré et al., 2001). Although we found that foraging frequency was similar in sites marked by jaguars and control sites, other components of foraging behavior, such as search or consumption time, may be affected by predation pressure. Examining the role of predator scent marks in predator-prey interactions would be useful to understand how predators influence patterns of prey abundance and distribution (Suraci et al., 2016; Taylor, 2013).

Our results are consistent with other research that show that scent marks of top predators can be detected by other species, inducing behavioral changes. We also found that jaguar feces are detected by 1) puma, the subordinate sympatric predator, 2) mesocarnivores, and

3) prey. We found that the detection of jaguar feces generates behavioral changes, according to the ecological interaction that each species has with the jaguar. This study is the first to analyze the effects of jaguar feces on the behavior of other species. However, more research is needed to understand the behavioral effects that triggers by jaguar feces and their implications at different ecological levels.

The presence of top predators such as the jaguar causes cascading effects down food webs potentially critical for conserving ecosystem function (Berger, 2010; Suraci et al., 2016). Cascading effects are triggered by direct killing of prey and by modifying the behavior of prey that perceive their presence (Mpemba et al., 2019; Schmitz et al., 1997; Schmitz et al., 2008). In this context, the feces deposition by top predators such as jaguar and its potential to modify the behavior of other species have great scope in terms of conservation.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

REFERENCES

Allen, B. L., Allen, L. R., Andren, H., Ballard, G., Boitani, L., Engeman, R. M., Fleming, P. J. S., Ford, A. T., Haswell, P., Kowalczyk, R. L., Linnell, J. D. C., Mech, L. D., & Parker, D. M. (2017). Can we save large carnivores without losing large carnivore science? *Food Webs*, *12*, 64–75.

Allen, M. L., Avrin, A. C., Wittmer, H. U., Wang, Y., & Wilmers, C. C. (2024). Mesocarnivores vary in their spatiotemporal avoidance strategies at communications hubs of an apex carnivore. *Oecologia*, *204*(4), 805–813.

Allen, M. L., Gunther, M. S., & Wilmers, C. C. (2017). The scent of your enemy is my friend? The acquisition of large carnivore scent by a smaller carnivore. *Journal of Ethology*, *35*, 13–19.

Allen, M. L., Rovero, F., Oberosler, V., Augugliaro, C., & Krofel, M. (2023). Effects of snow leopards (*Panthera uncia*) on olfactory communication of Pallas's cats (*Otocolobus manul*) in the Altai Mountains, Mongolia. *Behaviour*, *160*, 807–815.

Allen, M. L., Wittmer, H. U., Houghtaling, P., Smith, J., Elbroch, L. M., & Wilmers, C. C. (2015). The role of scent marking in mate selection by female pumas (*Puma concolor*). *PLoS ONE*, *10*(10), e0139087.

Allen, M. L., Wittmer, H. U., Setiawan, E., Jaffe, S., & Marshall, A. J. (2016). Scent marking in Sunda clouded leopards (*Neofelis diardi*): Novel observations close a key gap in understanding felid communication behaviours. *Scientific Reports*, *6*(1), 35433.

Altendorf, K. B., Laundré, J. W., López González, C. A., & Brown, J. S. (2001). Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy*, *82*(2), 430–439.

Apfelbach, R., Blanchard, C. D., Blanchard, R. J., Hayes, R. A., & McGregor, I. S. (2005). The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neuroscience and Biobehavioral Reviews*, *29*(8), 1123–1144.

Ávila-Nájera, D. M., Palomares, F., Chávez, C., Tigar, B., & Mendoza, G. D. (2018). Jaguar (*Panthera onca*) and puma (*Puma concolor*) diets in Quintana Roo, Mexico. *Animal Biodiversity and Conservation*, *41*(2), 257–266.

Bai, D., Kang, Y., Ruan, S., & Wang, L. (2021). Dynamics of an intraguild predation food web model with strong Allee effect in the basal prey. *Nonlinear Analysis: Real World Applications*, *58*, 103206.

Berger, J. (2010). Fear-mediated food webs. In J. Terborgh, & J. A. Estes (Eds.), *Trophic cascades: Predators, prey and the changing dynamics of nature* (pp. 241–253). Island Press.

Buesching, C. D., & Jordan, N. R. (2022). The function of carnivore latrines: Review, case studies, and a research framework for hypothesis testing. In E. Do Linh San, J. J. Sato, J. L. Belant, & M. J. Somers (Eds.), *Carnivore ecology and conservation: A handbook of techniques* (pp. 131–171). https://doi.org/10.1002/9781118943274.ch7

Ceballos, G., Zarza, H., Chávez, C., & González-Maya, J. F. (2016). Ecology and conservation of jaguars in Mexico. In A. Alonso-Aguirre, & R. Sukumar (Eds.), *Tropical conservation: Perspectives on local and global priorities* (pp. 273). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199766987.003.0013

Cornhill, K. L., & Kerley, G. I. (2020). Cheetah communication at scent-marking sites can be inhibited or delayed by predators. *Behavioral Ecology and Sociobiology*, *74*, 21.

Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, *25*(4), 773–784.

Davis, R. S., Yarnell, R. W., Gentle, L. K., Uzal, A., Mgoola, W. O., & Stone, E. L. (2021). Prey availability and intraguild competition regulate the spatiotemporal dynamics of a modified large carnivore guild. *Ecology and Evolution*, *11*(12), 7890–7904.

Edwards, S., Mueller, R., Roeder, R., Melzheimer, J., & Wachter, B. (2022). Cheetah marking sites are also used by other species for communication: evidence from photographic data in a comparative setup. *Mammalian Biology*, *102*(4), 1345–1356.

Elbroch, L. M., & Kusler, A. (2018). Are pumas subordinate carnivores, and does it matter? *PeerJ*, *6*, e4293.

Elbroch, L. M., & Quigley, H. (2017). Social interactions in a solitary carnivore. *Current Zoology*, *63*(4), 357–362.

Epperly, H. K., Clinchy, M., Zanette, L. Y., & McCleery, R. A. (2021). Fear of large carnivores is tied to ungulate habitat use: Evidence from a bifactorial experiment. *Scientific Reports*, *11*(1), 12979.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., & Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, *333*(6040), 301–306.

Ford, A. T. (2017). Opportunities and challenges for the study and conservation of large carnivores. *Food Webs*, *12*, 107–109.

Frantz, A. C., Pope, L. C., Carpenter, P. J., Roper, T. J., Wilson, G. J., Delahay, R. J., & Burke, T (2003). Reliable microsatellite genotyping of the Eurasian badger (*Meles meles*) using faecal DNA. *Molecular Ecology*, *12*(6), 1649–1661.

Hansen, K. W., Ranc, N., Morgan, J., Jordan, N. R., McNutt, J. W., Wilson, A., & Wilmers, C. C. (2024). How territoriality and sociality influence the habitat selection and movements of a large carnivore. *Ecology and Evolution*, *14*(4), e11217.

Harmsen, B. J., Foster, R. J., Silver, S. C., Ostro, L. E., & Doncaster, C. P. (2009). Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a neotropical forest. *Journal of Mammalogy*, *90*(3), 612–620.

Haswell, P. M., Jones, K. A., Kusak, J., & Hayward, M. W. (2018). Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. *Oecologia*, *187*, 573–583.

Herman, C. S., & Valone, T. J. (2000). The effect of mammalian predator scent on the foraging behavior of *Dipodomys merriami. Oikos*, *91*(1), 139–145.

Hoeks, S., Huijbregts, M. A., Busana, M., Harfoot, M. B., Svenning, J. C., & Santini, L. (2020). Mechanistic insights into the role of large carnivores for ecosystem structure and functioning. *Ecography*, *43*(12), 1752–1763.

Holdridge, L. (1967). *Clasificación de zonas de vida según el sistema de clasificación de Holdridge*. Centro Científico Tropical.

Houtman, A. (2003). The response of tree squirrels to conspecific and heterospecific alarm calls. B. J. Ploger, & K. Yasukawa (Eds.), *Exploring animal behavior in laboratory and field* (pp. 295–300). Academic Press.

Karanth, K. U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., & Kumar, N. S. (2017). Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1848), 20161860.

Kemna, C. J., Nagy-Reis, M. B., & Scrafford, M. A. (2020). Temporal segregation among sympatric boreal predators. *Mammal Research*, *65*(3), 565–572.

Kimbrell, T., Holt, R. D., & Lundberg, P. (2007). The influence of vigilance on intraguild predation. *Journal of Theoretical Biology*, *249*(2), 218–234.

Köppen, W. (1900). Attempt at a classification of climates, preferably according to their relationship to the flora. *Geographische Zeitschrift*, *6*(12), 657–679.

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, *79*(8), 1401–1409.

Lu, Q., Cheng, C., Xiao, L., Li, J., Li, X., Zhao, X., & Yao, M. (2023). Food webs reveal coexistence mechanisms and community organization in carnivores. *Current Biology*, *33*(4), 647–659.

Medellín, R. A., de la Torre, A., Zarza, H., Chávez, C., & Ceballos, G. (2016). *El jaguar en el siglo XXI: La perspectiva continental*. Ediciones Científicas Universitarias.

Miaretsoa, L., Cascella, A., Vadàla, L., Valente, D., De Gregorio, C., Torti, V., & Gamba, M. (2022). Marking versus overmarking: Spatial and behavioral patterns of scent marking in wild Diademed Sifaka (*Propithecus diadema*). *International Journal of Primatology*, *43*(4), 611–635.

Morehouse, A. T., Loosen, A. E., Graves, T. A., & Boyce, M. S. (2021). The smell of success: reproductive success related to rub behavior in brown bears. *PLoS ONE*, *16*(3), e0247964.

Mpemba, H., Yang, F., & Jiang, G. (2019). The implications of fear ecology for interactions among predators, prey and mesopredators. *Journal of Animal and Plant Sciences*, *29*(6), 1519–1527.

Müller, L., Briers-Louw, W. D., Amin, R., Lochner, C. S., & Leslie, A. J. (2022). Carnivore coexistence facilitated by spatial and dietary partitioning and fine-scale behavioural avoidance in a semi-arid ecosystem. *Journal of Zoology*, *317*(2), 114–128.

Murphy, L. B. (1978). The practical problems of recognizing and measuring fear and exploration behaviour in the domestic fowl. *Animal Behaviour*, *26*, 422–431.

Palomares, F., Fernández, N., Roques, S., Chávez, C., Silveira, L., Keller, C., & Adrados, B. (2016). Fine-scale habitat segregation between two ecologically similar top predators. *PLoS ONE*, *11*(5), e0155626.

Palomares, F., González-Borrajo, N., Chávez, C., Rubio, Y., Verdade, L. M., Monsa, R., & Zanin, M. (2018). Scraping marking behaviour of the largest Neotropical felids. *PeerJ*, *6*, e4983.

Pilgrim, K. L., McKelvey, K. S., Riddle, A. E., & Schwartz, M. K. (2005). Felid sex identification based on noninvasive genetic samples. *Molecular Ecology Notes*, *5*(1), 60–61.

Prugh, L. R., & Sivy, K. J. (2020). Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. *Ecology Letters*, *23*(5), 902–918.

Rafiq, K., Jordan, N. R., Meloro, C., Wilson, A. M., Hayward, M. W., Wich, S. A., & McNutt, J. W. (2020). Scent-marking strategies of a solitary carnivore: Boundary and road scent marking in the leopard. *Animal Behaviour*, *161*, 115–126.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484.

Roques, S., Adrados, B., Chávez, C., Keller, C., Magnusson, W. E., Palomares, F., & Godoy, J. A (2011). Identification of neotropical felid feces using RCP-PCR. *Molecular Ecology Resources*, *11*(1), 171–175.

Ruprecht, J., Eriksson, C. E., Forrester, T. D., Spitz, D. B., Clark, D. A., Wisdom, M. J., & Levi, T. (2021). Variable strategies to solve risk–reward tradeoffs in carnivore communities. *Proceedings of the National Academy of Sciences*, *118*(35), e2101614118.

Russell, J. C., Lecomte, V., Dumont, Y., & Le Corre, M. (2009). Intraguild predation and mesopredator release effect on long-lived prey. *Ecological Modelling*, *220*(8), 1098–1104.

Samuel, L., Arnesen, C., Zedrosser, A., & Rosell, F. (2020). Fears from the past? The innate ability of dogs to detect predator scents. *Animal Cognition*, *23*, 721–729.

Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology*, *78*(5), 1388–1399.

Schmitz, O. J., Grabowski, J. H., Peckarsky, B. L., Preisser, E. L., Trussell, G. C., & Vonesh, J. R. (2008). From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology*, *89*(9), 2436–2445.

Sheriff, M. J., Peacor, S. D., Hawlena, D., & Thaker, M. (2020). Non-consumptive predator effects on prey population size: A dearth of evidence. *Journal of Animal Ecology*, *89*(6), 1302–1316.

Smith, J. L. D., Mc Dougal, S., & Miquelle, D. (1989). Scent marking in free-ranging tigers, *Panthera tigris*. *Animal Behaviour*, *37*, 1–10.

Sommers, P., & Chesson, P. (2019). Effects of predator avoidance behavior on the coexistence of competing prey. *The American Naturalist*, *193*(5), E132–E148.

Spalinger, D. E., & Hobbs, N. T. (1992). Mechanisms of foraging in mammalian herbivores: New models of functional response. *The American Naturalist*, *140*(2), 325–348.

Srivathsa, A., Ramachandran, V., Saravanan, P., Sureshbabu, A., Ganguly, D., & Ramakrishnan, U. (2023). Topcats and underdogs: Intraguild interactions among three apex carnivores across Asia's forestscapes. *Biological Reviews*, *98*(6), 2114–2135.

Sunde, P., Böcker, F., Rauset, G. R., Kjellander, P., Chrenkova, M., Skovdal, T. M., & Heurich, M. (2022). Mammal responses to predator scents across multiple study areas. *Ecosphere*, *13*(8), e4215.

Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D., & Zanette, L. Y. (2016). Fear of large carnivores causes a trophic cascade. *Nature Communications*, *7*(1), 10698.

Tallian, A., Ordiz, A., Zimmermann, B., Sand, H., Wikenros, C., Wabakken, P., & Kindberg, J. (2021). The return of large carnivores: Using hunter observation data to understand the role of predators on ungulate populations. *Global Ecology and Conservation*, *27*, e01587.

Taylor, R. J. (2013). *Predation*. Springer Science and Business Media.

van Beeck-Calkoen, S. T., Kreikenbohm, R., Kuijper, D. P., & Heurich, M. (2021). Olfactory cues of large carnivores modify red deer behavior and browsing intensity. *Behavioral Ecology*, *32*(5), 982–992.

Wang, Y., Allen, M. L., & Wilmers, C. C. (2020). Mesopredators display behaviourally plastic responses to dominant competitors when scavenging and communicating. *bioRxiv*, *2020*, 913335.

Wooldridge, R. L., Foster, R. J., & Harmsen, B. J. (2019). The functional role of scent marking in the social organization of large sympatric neotropical felids. *Journal of Mammalogy*, *100*(2), 445–453.