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When waterholes get busy, rare interactions thrive: Photographic evidence of a jaguar (*Panthera onca*) killing an ocelot (*Leopardus pardalis*)

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Abstract

During a camera trap survey conducted in Guatemala in the 2019 dry season, we documented a jaguar killing an ocelot at a waterhole with high mammal activity. During severe droughts, the probability of aggressive interactions between carnivores might increase when fixed, valuable resources such as water cannot be easily partitioned.

KEYWORDS
activity overlap, activity patterns, carnivores, interspecific killing, drought, climate change, Maya forest, Guatemala

1 | INTRODUCTION

Interference competition is an important process working to shape mammalian carnivore communities (Palomares and Caro 1999; Donadio and Buskirk 2006). Dominance in these interactions is often asymmetric based on body size (Palomares and Caro 1999; de Oliviera and Pereira 2014), and the threat of intraguild strife from larger and more dominant carnivores has been found to alter resource use, distribution patterns, grouping, activity, and diet of subordinates (e.g., Carbone et al. 1997; Mills and Gorman 1997; Moreno et al. 2006; Jensen and Humphries, 2019; Shores et al. 2019). The top-down regulatory effects of apex predators on smaller carnivores can be profound, and loss of large predators can lead to "release" of smaller predators, with ramifications for the entire ecological community (Ritchie and Johnson 2009; Prugh et al. 2009).

Interspecific killing is an extreme form of interference competition in mammalian carnivores and may include either interspecific predation, where one species consumes the other, or interspecific killing more generally, where one species does not consume the other, but rather benefits from elimination of a competitor (Ritchie and Johnson 2009). Interspecific killing has been documented in many different pairs of carnivores and is more likely when the larger species is 2–5.4 times the mass of the victim species, or when the larger species is a hypercarnivore (Donadio and Buskirk 2006; de Oliveria and Pereira 2014). Carnivores may reduce the likelihood of these types of encounters through the partitioning of habitat or temporal activity. However, the presence of spatially fixed resources that cannot be easily partitioned, such as small habitat patches or carcasses, may increase the likelihood of aggressive interactions between carnivores by restricting or altering their use of space (Parsons et al. 2019; Allen et al. 2016). Waterholes are another spatially fixed resource that may promote interactions between carnivores (Atwood et al. 2011). Although typically studied in arid and savanna environments, waterholes may also be a scarce and valuable resource in seasonal Neotropical forests (Akpinar-Ferrand, 2011). Despite their potential importance, the use of waterholes by Neotropical carnivores remains largely unstudied. Here, we document clear photographic evidence of a jaguar (*Panthera onca*) killing an ocelot (*Leopardus pardalis*) at a waterhole located within a seasonal Neotropical forest (Figure 1).

Jaguar diet is diverse, varying as the prey community changes throughout its range. Prey body size ranges from small preys such as rabbits (*Sylvilagus brasiliensis*) (~1kg) and agoutis (*Dasyprocta sp.*) (~2kg) to prey as big as the lowland tapirs (*Tapirus terrestris*) (~130 kg) (Hayward et al., 2016). In the Maya forest, prey encountered at higher frequency in scats include armadillos (*Dasypus novemcintus*), coatis (*Nasua narica*) peccaries (*Pecari tajacu* and *Tayassu pecari*), and pacas (*Cuniculus paca*) (Novack et al., 2005; Weckel et al., 2006; Foster et al., 2010). The relative rarity of felids and other carnivorans in jaguar scats points to significant avoidance of this group of species as prey items (Hayward et al., 2016) and perhaps indicates only rare events of interspecific killing. Jaguars are the largest cat in the Americas. They are dominant over the other sympatric cats, particularly the next two largest species, the puma (*Puma concolor*) and ocelot. Given the size differential between jaguars and ocelots (jaguars are ~ 5–7 times the mass of ocelots), jaguars may be more likely to engage in interspecific killing of ocelots (de Oliveria and Pereira 2014). Jaguar scats containing ocelots or other species of the same genera are suggestive of interspecific killing (e.g., Chinchilla 1997; Taber et al. 1997; Gonzalez-Maya et al. 2010). Nevertheless, in these cases, the possibility of carrion consumption or misidentification of remains cannot be ruled out. We are also unaware of any direct observations of such interactions in the field, perhaps due to the elusive behavior of both species and the difficulty of observing interactions in the dense tropical forest. Our photographs are then direct and clear evidence of interspecific killing of ocelots by jaguars.

During 2018/2019, a spatially extensive camera-trapping study (covering 1583 km^2) was conducted in the Maya Biosphere Reserve of northern Guatemala (Supplementary Figure 1). As part of this project, some of the remote cameras were placed at waterholes (N = 89; 47 in 2018, 42 in 2019) to record species presence. Particularly during the dry season (December to June), these waterholes contain some of the last remaining surface water, as the porous nature of the karst landscape at the Maya forest prevents water retention beyond the rainy season. During the 2019 dry season, half (21 of 42) of the waterholes we sampled were

FIGURE 1 Photographic sequence of a jaguar (*Panthera onca*) attacking and apparently killing an ocelot (*Leopardus pardalis*) at a waterhole in northern Guatemala in March of 2019 (to see the entire sequence please refer to the Supplementary material). An adult male ocelot approaches a waterhole for a drink. As soon as the ocelot sits down to drink, an adult male jaguar attacks the ocelot, and three minutes later, it drags it away. The male jaguar had appeared at the waterhole a little over an hour prior to the ocelot and left the frame from the same side that it initiates its attack. Photographic credit: Mammal Spatial Ecology and Conservation Lab at Washington State University, Wildlife Conservation Society—Guatemala, Centro de Estudios Conservacionistas (CECON), and Consejo Nacional de Áreas Protegidas (CONAP)

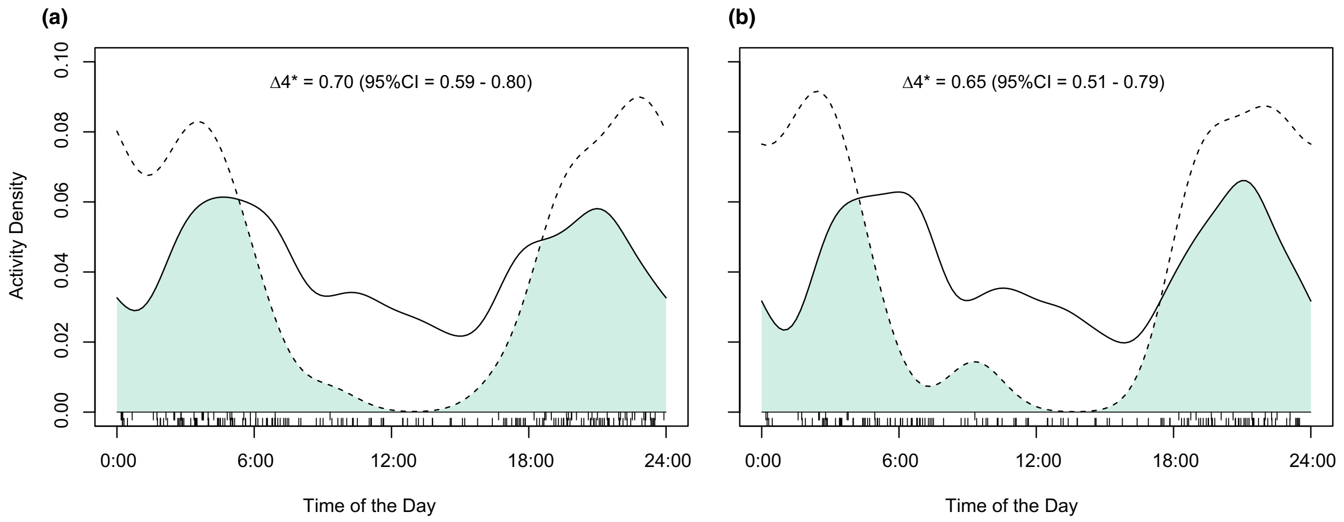

FIGURE 2 Temporal overlap between jaguars (*Panthera onca*) and ocelots (*Leopardus pardalis*) at waterholes, based on kernel density estimates from time-stamped camera images. Black solid lines show jaguar activity and the dashed line shows ocelot activity. X- and y-axis represent time of the day and activity density, respectively. Δ is the coefficient of overlap and goes from 0—no overlap—to 1—complete overlap. Number of events used per species per analysis are labeled as e_j and e_o for jaguars and ocelots, respectively. Panels represent different subsets of events included in the analysis: (a) Waterholes surveyed in 2019 (n = 42), (e_j = 142, e_o = 52). (b) Waterholes with water (n = 21) surveyed in 2019 (e_j = 128, e_o = 22). Jaguar and ocelot overlap largely occurred during crepuscular time periods. The interspecific killing event occurred at 19:39, during one of the two crepuscular periods of high temporal overlap between the species

dry due to a strong and persistent drought. As a result, mammal activity was remarkably concentrated at waterholes that retained water. The events reported here occurred in a waterhole (89.6058°W, 17.7713°N) with abundant water that was isolated from other nearby waterholes by almost 10 km (Figure S1). Our camera-trapping records at this waterhole revealed a busy hub of carnivore activity. In only three months of sampling at this one waterhole, our single camera recorded at least seven different individual jaguars, an encounter between two jaguars, seven different species of carnivores (out of the eight present in our study area), and most intriguingly, clear photographic evidence of a deadly interaction between two carnivores. On 31 March 2019, a male jaguar passes by the waterhole at 18:20, leaving toward the left side of the frame. At 19:28, an adult tapir (*Tapirus bairdii*) drinks from the waterhole and then leaves. Ten minutes later (19:39), an adult male ocelot (apparently healthy based on body appearance) approaches the waterhole and crouches down to drink (Figure 1 and Supplementary material). Just forty seconds after that, the same male jaguar enters from the left side of the frame, attacks the ocelot from behind, and drags it away, holding it firmly in its jaws (Figure 1). The entire killing event lasted approximately 3.5 minutes, from which we obtained two bursts of five pictures each, one at the moment of the attack and a second activation when the jaguar walked away from the waterhole. This sequence of events suggests that the jaguar was lying in wait. It seemingly passes up the opportunity to attack the tapir, perhaps due to the difficulty in killing such a large and potentially dangerous prey item.

Previous work examining interference competition at waterholes in other environments, suggests that subordinate species may alter their temporal patterns of visitation to decrease the potential interactions with the dominant species (Valiex et al., 2007; Atwood et al. 2011), especially when water resources are scarce enough to prevent spatial segregation (Edwards et al. 2015). We examined this and assessed whether there was a temporal segregation in the use of waterholes by jaguars and ocelots. We used camera trap time stamps to derive activity patterns for each species and a kernel density estimate as a measure of their temporal overlap (Meredith and Ridout 2018). This measure ranges from zero, indicating no temporal overlap in activity, to one indicating complete temporal overlap between the two species (Ridout and Linkie 2009). We estimated activity overlap between jaguars and ocelots for all waterholes, and only waterholes that did not dry out in 2019. We obtained an overlap estimate (Δ4) of 0.70 (95% CI = 0.59 – 0.80; events$(e)_{jaguars}$ = 142, $e_{ocelots}$=52) across all waterholes surveyed ($n_{waterholes}$ = 42), and a similar estimate of 0.65 (95% CI = 0.51 – 0.79; $e_{jaguars}$ = 128, $e_{ocelots}$= 22) for only waterholes that did not dry out ($n_{waterholes}$ = 21). In general, ocelots were more nocturnal than jaguars but there was substantial overlap in crepuscular time periods (Figure 2). Our data provide limited evidence of temporal segregation of the subordinate species. Observed overlap values from our study are similar to other estimates of temporal overlap between these species using similar methodology in different areas and/or ecosystems (e.g., Herrera et al. 2018; Santos et al. 2019).

Spatial segregation was also limited in our study area. For the 2019 sampling period, when ocelots visited a waterhole ($n_{distinct\ waterholes}$ = 18), jaguars also attended the same waterhole 72% of the time ($n_{distinct\ waterholes\ with\ both\ species}$= 13). Thus, ocelots may not be able to alter their spatial distribution and timing of attendance at waterholes enough to avoid occasional encounters with dominant competitors at these valuable resources.

In the scenario of severe dry seasons such as the one of 2019, waterholes and other water resources might become "hotspots" of interspecific interactions in seasonal Neotropical forests. Given the large number of prey species also present at waterholes, these landscape features may be hotspots of both predator–predator as well as predator–prey interactions (and we have a photo sequence of a jaguar chasing a young tapir at a waterhole). The average daily number of independent events of mammals (detections separated by more than half an hour) was 0.4 per day for 2018, while in the drier year 2019, the average value at waterholes that maintained water was 2.4 per day. The waterhole where we recorded the jaguar attack in 2019 had 5.9 mammal detections per day, likely due to its marked isolation from other water sources. Thus, while direct interspecific killing may be a rare event, competitive, and predator–prey interactions in general are likely enhanced at waterholes for the entire tropical mammal community, particularly in drought years.

The extent to which interactions at waterholes affect population dynamics of the species in question remains unknown. But we can predict that these events might be more frequent as the extent and severity of drought seasons intensify in the Maya forest and further restricts the number of water sources. This provides an interesting opportunity for the study of interactions among carnivores and how waterholes in seasonal tropical environments may help shape use of space, community dynamics, and movement of mammals, and may provide a keystone (and perhaps contested) resource during severe dry seasons. We therefore recommend further monitoring of water levels, species occupancy, and interactions at these isolated water sources. Our data also suggest negative impacts of severe droughts for wildlife populations in environments with limited water sources such as the Maya forest. In areas apart from local communities, where humans also utilize the same water resources (e.g., resource extraction campsites inside multi-use protected areas), we recommend avoiding the use of waterholes by humans during severe drought periods as this might have drastic negative consequences for Maya forest wildlife communities.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The Editor-in-Chief has waived the required archiving due to privacy or ethical restrictions https://doi.org/10.5061/dryad.4tmpg4f87.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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