The functional role of scent marking in the social organization of large sympatric neotropical felids

Rebecca L. Wooldridge,[*] Rebecca J. Foster, and Bart J. Harmsen

Panthera, 8 West 40th Street, 18th Floor, New York, NY 10018, USA (RLW, RJF, BJH)
Environmental Research Institute, University of Belize, University Drive, P.O. Box 340, Belmopan, Belize (RLW, BJH)
School of Biology, University of Leeds, Leeds LS2 9JT, UK (RLW)

* Correspondent: rwooldridge@panthera.org

Communication is an integral part of animal behavior, impacting population structure and individual fitness and regulating spatial distributions. Scent marking is common among solitary, low-density, and wide-ranging carnivores, such as felids. Understanding the functional role of scent marking will inform our understanding of the behavioral ecology of carnivores. We investigated patterns of scent marking by pumas (*Puma concolor*) and jaguars (*Panthera onca*) via weekly surveys of trails for scrapes and documenting scent-marking behaviors and responses using motion-triggered video cameras. Jaguars mainly sprayed vegetation, whereas pumas mainly scraped the ground. Only a subset of individuals for both pumas and jaguars were responsible for the majority of scent-marking activity. On average, male pumas scraped more frequently (scrapes/km) than male jaguars, and the scrape rate of male pumas increased following the presence of potential mates and competitors. Male pumas returned to trails more quickly following the presence of conspecifics (potential competitors or mates) than in their absence, however, visitation by male jaguars increased in response to competitors only. A male puma detected travelling with three different females on separate occasions scraped more frequently than males who were not detected with females. This study suggests that jaguars and pumas are constantly assessing, and reacting to, the presence and marks of competitors and potential mates, facilitating the maintenance of complex social structures.

La comunicación es una parte integral del comportamiento animal; la cual impacta la estructura de la población, la aptitud de adaptación individual y regula la distribución espacial. La marcación olfativa es común entre los carnívoros solitarios, de baja densidad y amplia distribución, como los felinos. El entender el papel funcional de la marcación con olores, informa nuestra comprensión de la ecología del comportamiento de los carnívoros. Investigamos los patrones de marcación de olor por pumas (*Puma concolor*) y jaguares (*Panthera onca*) a través de muestreos semanales de senderos con rastros de rasguños, documentando los comportamientos y respuestas de marcación de olor utilizando cámaras de video activadas por movimiento. Los jaguares rociaban principalmente la vegetación, mientras que los pumas predominantemente hicieron rasguños en el suelo. Solo un subconjunto de individuos, tanto de pumas como de jaguares, fueron responsables de la mayoría de la actividad de marcación de olores. En promedio, los pumas machos rasguñaron con mayor frecuencia (rasguños /km) que los jaguares machos, y la tasa de rasguñar se incrementó luego de la presencia de parejas potenciales y de competidores. Los pumas machos regresaron a los senderos más rápidamente siguiendo la presencia de con-específicos (potenciales parejas o competidores) que en su ausencia; sin embargo, la visita de jaguares machos se incrementó sólo en respuesta a los competidores. Un puma macho que se detectó viajando con tres hembras diferentes en distintas ocasiones, rasguñaba con mayor frecuencia que los machos que no fueron detectados con hembras. Este estudio sugiere que jaguares y pumas, constantemente están evaluando y reaccionando, a la presencia y las marcas de las potenciales parejas y competidores, facilitando el mantenimiento de estructuras sociales complejas.

Key words: communication, interspecific, jaguar, puma, scent marking, scraping

Populations of solitary species, including many felids, are often widely dispersed and thus communicate indirectly with conspecifics (Seidensticker et al. 1973; Smith et al. 1989; Bailey 1993; Logan and Sweanor 2001, 2010, Harmsen et al. 2010a; Allen et al. 2016b). Felids commonly leave scent marks and visual signals, allowing individuals to gain indirect information about conspecifics within an area following the production of the signal (Logan and Sweanor 2001, 2010; Sunquist and Sunquist 2002; Harmsen et al. 2010a, 2016; Allen 2014; Vogt et al. 2016). The functional role of scent marking includes advertising to potential mates and mate selection, asserting dominance within an area, and maintaining territories (Bailey 1974; Smith et al. 1989; Vogt et al. 2014; Allen et al. 2015, 2016c). Given the potential diverse functions of scent marking, it is important to understand how scent-marking dynamics may be influenced by factors such as the presence of conspecifics, or interspecific competitors.

Recently, advances have been made in our knowledge of the role of scent marking in felid social structure. Adult males scent mark more frequently than females or juveniles, and marking rates of adult males are associated with their residency status (Allen et al. 2014; Vogt et al. 2014). Temperate adult male pumas (*Puma concolor*) return sooner to specific marking locations in response to conspecific presence (Allen et al. 2016c). Behavioral responses may vary with male or female presence; for example, Allen et al. (2016c) found that male pumas increased the time spent at marking locations in response to other males, but not females. Female pumas visit these locations as assessors of male scent marks, choosing males with the highest production of signals (Allen et al. 2015). However, our current understanding of scent-marking dynamics and its functional role in felid social structure comes from studies on just two species that occur in the Northern Hemisphere: pumas and Eurasian lynx (*Lynx lynx*). Currently, no study has systematically investigated the functional role of scent marking in a tropical system, or where there are two similar-sized sympatric felids. In this study, we used video and camera traps to study scent marking in neotropical pumas and jaguars (*Panthera onca*) in Belize, Central America.

To date, studies on large neotropical felids have detailed the types and patterns of scent marks; see Allen et al. (2016b) for a review. Scraping is the main form of communication used by pumas, while rolling is more commonly used by jaguars (Harmsen et al. 2016). Within the neotropics, jaguar and puma ranges overlap extensively (Scognamillo et al. 2003; Harmsen et al. 2009; de la Torre et al. 2017), providing the opportunity to investigate interspecific responses to scent marks. Jaguars are larger than pumas and considered the top predator (Iriarte et al. 1990; Harmsen et al. 2010a). Scent-marking behavior by pumas may differ between the temperate zone, where they are the largest felid, and the neotropics, where they co-exist with the larger jaguar. Previous studies have found avoidance between jaguars and pumas, and an absence of pumas from locations where jaguars frequently scent mark (Harmsen et al. 2009, 2016). As scent marks provide a visual and olfactory record of individual presence (Vogt et al. 2016), pumas may alter their

scent-marking patterns, or the types of scent marks used, in the presence of larger co-existing carnivore species as a mechanism of avoidance. Comparison between marking dynamics of pumas in neotropical and temperate systems may also offer insights into whether scent-marking behaviors adapt to the environment, or are evolutionarily fixed regardless of geographic location or community composition.

Individuals may preferentially scent mark in areas where these marks have a high probability of being found by conspecifics. Allen et al. (2014) showed that the visual component of the scent mark is used by pumas to locate scrapes, whereas the urine component conveys the signal (Vogt et al. 2016). As such, trails are preferentially selected as marking locations (Vogt et al. 2014; Krofel et al. 2017). However, a by-product of this is the possibility of eavesdropping by other species. For example, interspecific competitors, such as jaguars and pumas, may use scent marks to avoid one another, while prey species may use scent marks to gain information on the presence of predators (Allen et al. 2016a; King et al. 2016). Whether large neotropical felids investigate the scent marks of their interspecific competitors is unclear, as is whether these scent marks are investigated by prey species or other smaller co-existing carnivore species.

We recorded spatial and temporal patterns of scent marks via surveys of trails that were matched to individual felids detected by camera traps. We placed video cameras at locations with a high frequency of marking activity to document scent-marking behaviors and responses. Based on a pilot study by Harmsen et al. (2016), we predicted that both jaguars and pumas would investigate scent marks of conspecifics, but only dominant resident individuals of both sexes would counter-mark. We predicted that visitation and scent-marking rates would increase in response to increased presence of conspecifics of either sex, to signal to competitors and potential mates, and that female mate choice would vary with male scent-marking activity. Additionally, we investigated to what extent other species investigated and responded to jaguar, puma, and ocelot (*Leopardus pardalis*) scent marks.

MATERIALS AND METHODS

Study area.—The study focused on a ~10 km² area within the eastern half of the Cockscomb Basin Wildlife Sanctuary in Belize, Central America (16°47′N/88°36′W). The basin was logged until the 1980s. It received protected status in 1986 and now comprises 425 km² of lowland subtropical moist broadleaf forest. It forms part of the Maya Mountain Massif, the largest contiguous forest block in Belize (Rabinowitz and Nottingham 1986; Harmsen et al. 2010c). Elevation ranges from 50 to 1,133 m. Yearly rainfall averages 2,700 mm, with most falling during the wet season (June to December), and the mean annual temperature is 25°C, but fluctuating by ~5°C between the warmest (April to June) and coolest (November to January) months (Kamstra 1996; Weckel et al. 2006).

Scrape surveys.—We surveyed for scrape activity along three trails (former logging roads, now tourist trails with

no vehicular traffic; width 2–5 m, length 2.7–8.6 km). Two researchers walked either side of the trails scanning the ground. We surveyed each trail every day for 20 consecutive days (daily survey), and every week for 13 weeks (weekly survey), from May to September 2016. We identified scrapes as a raked pile of leaves and soil at one end, with a visible patch of soil often partitioned by a ridge in the middle, and recorded the length, width, and UTM location. We avoided repeat counting of the same scrapes by placing small sticks at the base of the scrape. To understand degradation of visible scrape characteristics, we took photographs of 11 scrapes from day 1 up to a maximum of 35 days after the creation of the scrape. For each photo, we ranked the visibility of the soil patch (as a percentage of the original visible soil), and visibility of the pile on a scale from 0 (no pile visible) to 5 (pile as visible as on day zero), per weekly survey. We used our data on scrape degradation to set a temporal threshold above which we assumed that scrapes could no longer be detected.

We deployed 20 camera traps (Pantheracam V4 and V6; Panthera, New York, New York) ~700 m apart along the three survey trails and set them to monitor continuously (2,060 trap-nights; Fig. 1). We also deployed 23 video traps (Browning Strike Force; Browning Trail Cameras, Birmingham, Alabama) at 'scrape clusters' (Fig. 1), locations having more than three scrapes per 9 m^2 (Allen et al. 2014). From May until September 2016, we rotated the video traps to new locations after 3 weeks if there was no activity; thereafter, we left video traps filming the same scrape cluster until July 2017 (9,420 trap-nights). We set video to record maximally for 30 s in daylight and 10 s at night, both with an enforced 1-s delay between consecutive triggers.

For each camera trap, we assigned the adjacent 350 m of trail in either direction and considered scrapes in each 700-m section to be associated with the cats detected by the

Fig. 1.—Survey area in the Cockscomb Basin Wildlife Sanctuary showing locations of stationary cameras (n = 20) and scrape clusters monitored by video cameras (n = 30). Stationary cameras remained active from May 2016 to September 2016 (n = 103 days). Video cameras were rotated between scrape clusters from May to September 2016 based on activity (n = 103 days). Beyond September, 23 video cameras were left filming scrape clusters until July 2017 (n = 326 days). The panel in the bottom left corner indicates the location of the Cockscomb Basin Wildlife Sanctuary in Belize, and the location of the study area in the Cockscomb Basin Wildlife Sanctuary.

corresponding camera trap. The use of 700-m segments was a trade-off between the size of the segment and the size of the study area, with the number of camera traps available. Previous work identifying trail use by jaguars and pumas showed individuals of both species captured on consecutive cameras spaced 1 km apart, defined as a "walk," therefore, the camera spacing was suitable to associate individual cat detections with scrape locations per segment (Harmsen et al. 2010b). Hereafter, we refer to "segment-day" as a 700-m trail section from a daily survey, and "segment-week" as a 700-m trail section from a weekly survey. We used both the camera and video data to identify felid presence, abundance, and activity along the trails. We analyzed video data for communication behaviors, specifically scraping, spraying, rolling, or rubbing, and investigatory behaviors, specifically olfactory investigation and flehmen response, recording the species, sex, individual, date, and time. Additionally, we analyzed video data for detections of other species and recorded the investigation rate (n investigatory events/total n detections), per species. We only used detections of species that occurred within 28 days of a scent mark, due to visual and olfactory degradation of scent mark characteristics beyond this time. We excluded the paca (*Paca cuniculus*; n = 11 detections), nine-banded armadillo (*Dasypus novemcinctus*; n = 30 detections), hog-nosed skunk (*Conepatus leuconotus*; n = 50 detections), and common opossum (*Didelphis virginiana*; n = 123 detections), as we could not reliably distinguish between foraging and investigatory behaviors.

We assigned individual identifications to jaguars using the animal pattern recognition software "HotSpotter," which matches individuals unique rosette flank patterns (Crall et al. 2013). For pumas, we used unique scars and markings, parasites including visible swelled patches that emerge with botfly (*Dermatobia hominis*) growth, and by the presence of a GPS collar (Harmsen 2006; Kelly et al. 2008). We assigned sex via the presence or absence of visible testicles (Harmsen 2006). For each camera and video location, we calculated the abundance (number of individuals detected) and activity (number of detections) of jaguars and pumas.

Statistical analyses.—We used R version 3.3.2 (R Core Team 2013) and set a significance value of P < 0.05 for all statistical analyses. To investigate interspecific variation in scrape rate, we compared the scraping activity (n scrapes/individual/ segment-day or segment-week) of male jaguars and male pumas using a Mann–Whitney U-test. We excluded segment-occasions (n = 99) for which multiple individuals or species were detected within a segment between surveys (day or week), using only those segment-occasions (n = 102) in which a single male jaguar or puma had been present.

To investigate variation in return interval and marking behavior with the presence of conspecifics, we tested whether "individual return interval" (time interval in days between consecutive visits to a segment by an individual) of male jaguars or male pumas, and "individual scrape rate" (number of scrapes/individual/segment-week) of male pumas varied with the presence or absence of male and female conspecifics up to
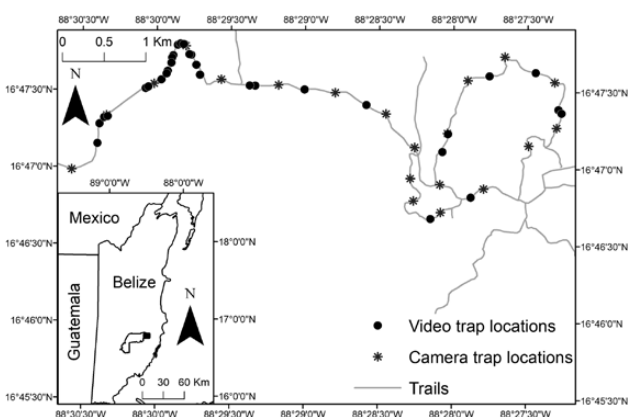
28 days prior. We could not conduct these analyses for females of either species due to low sample sizes. We removed incidences of duplicated return-interval associations based on pairs of individuals walking in consecutive segments within a single walk (Harmsen et al. 2010b) to eliminate any autocorrelation from the dataset. We used generalized linear mixed effect models with a Poisson distribution and a log link, with male and female presence within the previous 28 days as our fixed predictor variable, and returning individual ID as the random effect, in the program *lme4* (Bates et al. 2015). We tested data for overdispersion using *blmeco* (Korner-Nievergelt et al. 2015) and included an additional observation-level random effect (Harrison 2014) due to overdispersion in all datasets (individual return interval or individual scrape rate = conspecific presence + returning individual ID + observation level). To test for significance of our fixed predictor variable, we used a likelihood ratio test (Bolker et al. 2009) to compare the model with a null model using *lmtest* (Zeileis and Hothorn 2002). As we found limited visible evidence of jaguar marking events (e.g., scrapes), we limited all subsequent analyses of marking behavior to pumas.

To investigate variation in puma investigatory and marking behavior at scrape clusters, we tested whether the proportion of visits during which individuals displayed investigatory behaviors (sniffing, flehmen), or marking behaviors (scraping, rolling or rubbing, urinating), differed between males and females, or between resident and transient males, using chi-square tests. Following Harmsen et al. (2017), we defined male individuals as resident or transient based on their activity on the trails. We classified residents as those with a mean detection rate of > 1.7 per location, and transients as those with a mean detection rate of < 1 per location during the survey (Harmsen et al. 2017). Additionally, we tested whether the frequency of investigatory behavior by males varied with the presence of conspecifics. Specifically, we tested for variation in sniffing rate, flehmen rate, and rolling or rubbing rate. We used chi-square tests to test whether the proportion of visits during which each behavior was displayed was associated with the presence or absence of males and females within the previous 28 days. If sample sizes were < 5, we used Fishers Exact tests and report the *P*-value only.

To investigate female mate choice, we used data associated with those female pumas detected travelling with males during the study (Allen et al. 2015). We tested whether female puma mate choice (whether or not a male was detected with a female) varied with male scrape-marking activity (*n* scrapes/700 m/potential temporal detection window) prior to the pairing, using a general linear model with a binomial distribution (female puma mate choice = scrape-marking activity) using *lme4* (Bates et al. 2015). We tested the significance of our fixed predictor variable by using a likelihood ratio test (Bolker et al. 2009) to compare the model to a null model using *lmtest* (Zeileis and Hothorn 2002). We used data from 28 days prior to the first detection of a female in a segment, to the last detection of a female in the segment before the female and male were detected travelling together.

RESULTS

We monitored 50 locations (20 camera traps and 30 video traps; Fig. 1) between May 2016 and July 2017 (*n* = 9,911 functional trap days, $\overline{X} \pm SE$ = 198 ± 17.8 functional days per location, range = 22–410).

We recorded a total of 676 jaguar detections, of which 663 were identified to individual across 49 of the 50 locations. We identified 22 jaguars: nine females (167 detections), seven males (455 detections), five juveniles (40 detections), and one individual of unknown sex (one detection). Mean detection rate (detections/100 trap-nights/camera trap) of jaguars was 7.9 ± 0.9 ($\overline{X} \pm SE$; range 2–38) detections per location. Mean abundance (*n* individuals/100 trap-nights/camera trap) of jaguars was 3.3 ± 0.3 ($\overline{X} \pm SE$; range 2–8).

We recorded a total of 902 puma detections, of which 898 were identified to individual level across 42 of the 50 locations. We identified 16 pumas: 10 males (830 detections) and six females (68 detections). Mean detection rate of pumas from camera traps was 6.3 ± 1.2 ($\overline{X} \pm SE$ range 0–29) detections per location. Mean abundance of pumas was 1.7 ± 0.2 ($\overline{X} \pm SE$; range 0–6) individuals per location.

In the monitored scrapes (*n* = 11), soil visibility degraded faster than the pile. After 7 days, median soil visibility was 40% and pile visibility ranked 3 (where a rank of 0 is no longer visible). After 28 days, soil was no longer visible in any of the monitored scrapes, and the pile was just visible (lowest visibility ranking) in 27% of the scrapes. Median time to no soil visibility was 14 days (range 7–28 days). The shortest number of days to no pile visibility was 21 days (*n* = 3). On this basis, we assumed that scrapes no longer held a signaling function 28 days after creation.

We found 703 scrapes during the study ($\overline{X} \pm SE$ = 1.9 ± 0.23 scrapes/700 m/week, range 0–21). Of these, 190 were scrapes found during the baseline survey and so could not be attributed to species or individuals. There were 10 segment-weeks, and 13 segment-days, when scrapes were found but no jaguar or puma had been detected in the previous week or day (*n* = 26 scrapes). Of scrapes that could be assigned to individuals from both daily and weekly surveys (*n* = 224), 88% were attributed to two male resident pumas (Table 1). Marking frequency by male pumas was high: we detected scrapes in 82% of segment-occasions (*n* = 55) for which male pumas were the only large felid present. Scraping frequency by male jaguars was lower: we detected scrapes in 27% of segment-occasions (*n* = 47) in which male jaguars were the only large felid present. For females, we detected scrapes in 29% of occasions when female pumas were the only large felid present (*n* = 7), and 7% of occasions when female jaguars were the only large felid present (*n* = 36).

We detected 236 marking events at video traps by three species: pumas, jaguars, and ocelots. We detected 221 marking events by pumas (Table 2). Of these, 85% were scrapes and 14% were rubbing or rolling events by males, and 1% were by female pumas, who urinated on scrapes made by male pumas (Table 2). Additionally, we detected six marking events by jaguars, and nine marking events by ocelots. Spraying was the

Table 1.—Numbers of scrapes attributed to jaguar (*Panthera onca*) and puma (*Puma concolor*) individuals by matching cat detection on camera traps to scrape locations from 13 consecutive weekly surveys and 20 consecutive daily surveys in the Cockscomb Basin Wildlife Sanctuary, Belize.

Species	Sex	ID	Status[a]	*n* scrapes (segment-weeks)	*n* scrapes (segment-days)	Total
Jaguar (*Panthera onca*)	M	M1	Resident	13	1	14
	M	M2	Resident	3	1	4
	M	M3	Transient	2	2	4
	F	F1		3		3
	F	F2		2		2
	Unknown	NPD		4	1	5
Puma (*Puma concolor*)	M	M1	Resident	72	15	87
	M	M2	Resident	44	65	109
	M	NPD		22		22
	F	F2		1		1
	F	NPD		1		1
	Unknown	NPD		3		3
Jaguar or puma	M	NPD		126		126
Jaguar or puma	Unknown	NPD		95	11	106
Total				391	96	487

[a] Resident defined as having a mean detection rate > 1.7 per location during the survey; transient defined as mean detection rate < 1 per location, following Harmsen et al. (2017).

Table 2.—The frequency (%) and types of scent marks detected at scrape clusters (*n* = 30) by jaguar (*Panthera onca*), puma (*Puma concolor*), and ocelot (*Leopardus pardalis*) individuals in the Cockscomb Basin Wildlife Sanctuary, Belize.

Species	Sex	ID	Status[a]	Scrapes	Rubbing or rolling	Sprays	Urine	Total
Jaguar (*Panthera onca*)	M	M1	Resident	1 (0.4)		3 (1.3)		4 (1.7)
	M	M2	Resident		1 (0.4)	1 (0.4)		2 (0.8)
Puma (*Puma concolor*)	M	M1	Resident	117 (49.6)	13 (5.5)			130 (55.1)
	M	M2	Resident	68 (28.8)	16 (6.8)			84 (35.6)
	M	M3	Transient	1 (0.4)				1 (0.4)
	M	M4	Transient	2 (0.8)	2 (0.8)			4 (1.7)
	F	F1					1 (0.4)	1 (0.4)
	F	F2					1 (0.4)	1 (0.4)
Ocelot (*Leopardus pardalis*)	M	M1				8 (3.4)		8 (3.4)
	F	F1					1 (0.4)	1 (0.4)
Total				189 (80.1)	32 (13.5)	13 (5.5)	2 (0.8)	236 (100)

[a] Resident defined as having a mean detection rate > 1.7 per location during the survey; transient defined as mean detection rate < 1 per location, following Harmsen et al. (2017).

most common marking behavior detected for jaguars and ocelots, comprising 67% of jaguar scent marks and 100% of ocelot scent marks (Table 2).

We detected 265 incidences of investigatory behavior at video traps by nine species. We detected 236 incidences of investigatory behavior by pumas. Of these, 98% were sniffing and 2% flehmen, with two resident male pumas responsible for 89% of sniffing events, and 100% of flehmen events. Of the remaining 23 sniffing events, 65% were by female pumas, and 35% by transient males. We detected 29 incidences of interspecific investigation of scent marks by nine species (Table 3). Fourteen species were detected at scrape clusters within 28 days of a puma scent mark, and we detected investigatory behavior from eight (Table 3). Of the non-puma species, collared peccaries (*Pecari tajacu*) had the highest investigation rate of puma scent marks (Table 3). Additionally, we detected one incidence of scent transference in the form of a tayra (*Eira barbara*) rubbing its head and neck in the scat of a puma.

We detected five species at video traps within 28 days of a jaguar scent mark and recorded investigatory behavior from three (Table 3). This included a puma investigating a jaguar scrape, but not sprays, and ocelots investigating jaguar sprays and scrapes. We detected 10 species at video traps within 28 days of ocelot scent marks and recorded one incidence of investigation by a coatimundi (*Nasua nasua*; Table 3). We did not detect jaguars investigating scent marks of pumas or ocelots, despite recording their repeated presence at scrape clusters (Table 3) and detected no evidence of interspecific countermarking by any species.

Interspecific variation in scrape rate.—From the camera-trap data, we assigned scrapes to pumas at a higher rate than to jaguars (male puma $\overline{X} \pm SE$: 3.6 ± 0.4 scrapes/700 m, range 0–14; male jaguar $\overline{X} \pm SE$: 0.3 ± 0.1 scrapes/700 m, range 0–3; $W = 0.75$, $P < 0.0001$, $n = 47$ jaguar and 55 puma segment-weeks), giving an average of 5.1 ± 0.6 ($\overline{X} \pm SE$) scrapes/km for male puma individuals and 0.4 ± 0.1 ($\overline{X} \pm SE$) scrapes/km for male jaguar individuals.

Variation in return interval and marking behavior with the presence of conspecifics.—Due to autocorrelation from pairs of individuals travelling between consecutive segments within a single walk, we removed 79 return intervals for male puma presence, 52 for female puma presence, 51 for male jaguar

Table 3.—The number of investigatory events (IE), number of detections (D), and the interspecific investigation rate (IIR—n investigatory events/total n detections) of neotropical mammals at video traps placed at scrape clusters ($n = 30$) in the Cockscomb Basin Wildlife Sanctuary, Belize. Only detections within 28 days of a scent mark were used due to degradation of visual and olfactory scent mark characteristics. NA = not applicable.

| Species	Jaguar scent marks			Puma scent marks			Ocelot scent marks		
	IE	D	IIR	IE	D	IIR	IE	D	IIR
Panthera onca	NA	NA	NA	0	154	0	0	5	0
Leopardus pardalis	2	2	1	5	85	0.1	NA	NA	NA
Leopardus weidii				2	14	0.1			
Puma concolor	1	8	0.1	NA	NA	NA	0	11	0
Puma yaguaroundi				3	6	0.5	0	1	0
Urocyon cinereoargenteus				1	4	0.3			
Nasua nasua				1	9	0.1	1	1	1
Procyon lotor				0	2	0			
Eira barbara	0	1	0	2	24	0.1	0	3	0
Galictis vittata				0	1	0			
Tayassu pecari				0	5	0	0	1	0
Pecari tajacu				5	8	0.6	0	2	0
Mazama americana	1	2	0.5	5	28	0.2	0	2	0
Tapirus terrestris	0	1	0	0	27	0	0	3	0
Tamandua mexicana				0	3	0			
Total	4	14		24	370		1	29	
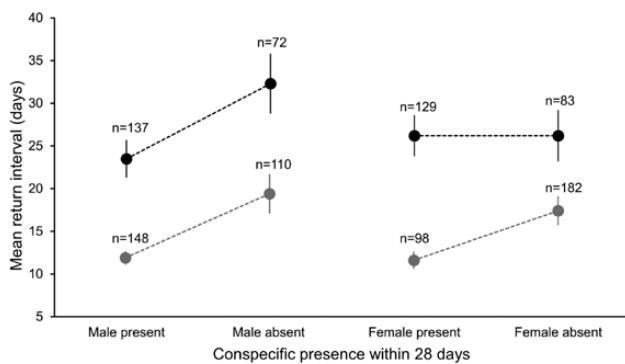
Fig. 2.—The return interval (time interval in days between consecutive visits to trail segments by an individual) of male pumas (*Puma concolor*; gray circles) and male jaguars (*Panthera onca*; black circles) in response to the presence and absence of conspecific males and females within the previous 28 days, in the Cockscomb Basin Wildlife Sanctuary, Belize. Bars indicate *SE*. Male pumas returned sooner in response to male presence ($X^2_1 = 5.0$, $P < 0.05$) and female presence ($X^2_1 = 3.9$, $P = 0.05$), male jaguars returned sooner in response to male presence ($X^2_1 = 5.5$, $P < 0.05$).
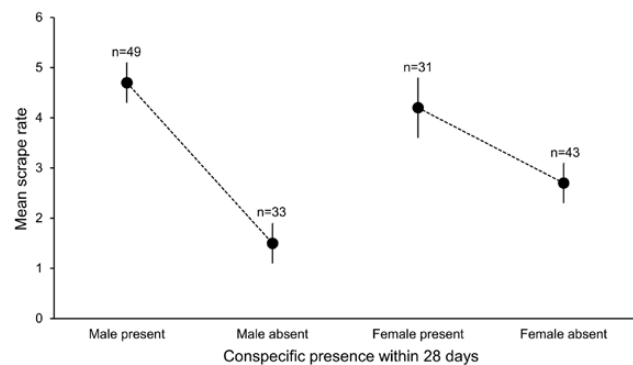

Fig. 3.—The scrape rate (number of scrapes/individual/segment-week) of male pumas (*Puma concolor*) in response to the presence and absence of conspecific males and females within the previous 28 days, from 13 weekly and 20 consecutive daily scrape surveys in the Cockscomb Basin Wildlife Sanctuary, Belize. Bars indicate *SE*. Scrape rate of male pumas increased in response to male presence ($X^2_1 = 29.4$, $P < 0.0001$) and female presence ($X^2_1 = 4.8$, $P < 0.05$).

presence, and 50 for female jaguar presence. For pumas, males returned on average 6.0 days sooner when another male had been present within the past 28 days, than when another male had not been present (return interval, male presence $\overline{X} \pm SE$: 12.5 ± 1.0 days, male absence $\overline{X} \pm SE$: 18.5 ± 2.4; $X^2_1 = 5.0$, $P < 0.05$, $n = 148$ present, 110 absent; Fig. 2), and on average 4.5 days sooner when a female had been present within the past 28 days (return interval, female presence $\overline{X} \pm SE$: 12.4 ± 1.2 days, female absence $\overline{X} \pm SE$: 16.9 ± 1.6; $X^2_1 = 3.9$, $P < 0.05$, $n = 98$ present, 182 absent; Fig. 2). For jaguars, males returned on average 7.3 days sooner when another male had been present within the previous 28 days (return interval, male presence $\overline{X} \pm SE$: 23.7 ± 2.4 days, male absence $\overline{X} \pm SE$: 31.1 ± 3.7; $X^2_1 = 5.5$, $P < 0.05$, $n = 137$ present, 72 absent; Fig. 2);

however, there was no evidence that they returned sooner when a female had been present ($X^2_1 = 0.2$, $P > 0.05$, $n = 129$ present, 83 absent; Fig. 2).

Individual scrape rate by male pumas increased with the presence of conspecifics, approximately tripling when another male had been present within 28 days, than when another male had not been present (scrape rate, male presence $\overline{X} \pm SE$: 4.7 ± 0.4 scrapes/700 m, male absence $\overline{X} \pm SE$: 1.5 ± 0.4; $X^2_1 = 29.4$, $P < 0.0001$, $n = 49$ present, 33 absent; Fig. 3), and approximately doubling when a female had been present within 28 days (female presence $\overline{X} \pm SE$: 4.2 ± 0.6 scrapes/700 m, female absence $\overline{X} \pm SE$: 2.7 ± 0.4; $X^2_1 = 4.8$, $P < 0.05$, $n = 31$ present, 43 absent; Fig. 3).

Variation in puma investigatory and marking behavior at scrape clusters.—When visiting scrape clusters, male pumas were more likely to mark than females (males: 35% visits,

females: 6%, $P < 0.001$, $d.f. = 1, 595$; Fig. 4), and resident males were more likely to mark when visiting these sites than transient males (residents: 36% visits, transients: 11%, $P < 0.01$, $d.f. = 1, 563$; Fig. 4). We found no evidence of sex differences in the frequency of investigatory behaviors when pumas visited scrape clusters (males: 39% visits, female: 47%; $X^2_{1,595} = 0.5$, $P > 0.05$; Fig. 4), or between resident male pumas and transient male pumas (residents: 40% visits, transients: 30%; $X^2_{1,563} = 0.7$, $P > 0.05$; Fig. 4).

When a conspecific had been present in the previous 28 days, males pumas sniffed more frequently compared to when no conspecific had been present (male presence: $X^2_{1,566} = 12.4$, $P < 0.01$; female presence: $X^2_{1,511} = 3.7$, $P < 0.05$; Fig. 5). We found no evidence of an association between the frequency of flehmen or rubbing and rolling with presence of a conspecific ($P > 0.05$ for all; Fig. 5).

Variation in male–female pairing of pumas with male puma scraping activity.—We detected five potential mating events on video for jaguars ($n = 2$) and pumas ($n = 3$). For jaguars, two resident males were observed travelling with the same adult female on separate occasions and displaying courtship behavior. These individuals were the only males documented on camera scent-marking during the study out of seven detected males (Table 2).

For pumas, one resident male was detected travelling with each of three females and displaying courtship behavior. This male scraped more often than males who were not detected with females (scrape-marking activity, "selected" male $\overline{X} \pm SE$: 7.1 ± 1.8 scrapes/700 m, "unselected" males $\overline{X} \pm SE$: 1.5 ± 0.8; $X^2_1 = 9.4$, $P < 0.01$, $n = 21$ segments "selected" male, 42 segments "unselected" males).

DISCUSSION

Scent marking is an integral part of behavior in solitary and spatially dispersed mammals such as felids, regulating social hierarchies and mate c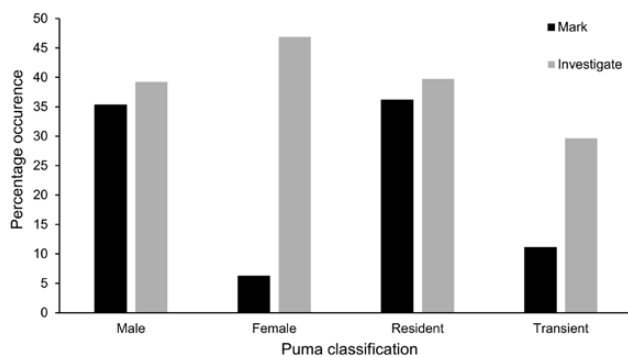hoice, and subsequently impacting population structure (Allen et al. 2014, 2015, 2016c; Vogt et al. 2014). Spraying on vegetation was the most common form of scent marking recorded for jaguars, whereas they scraped infrequently compared to pumas. As documented in the temperate zone, scraping on the ground was the primary means of marking for pumas. The scrape rates documented here for pumas are among the highest scent-marking rates recorded for any large felid species, with only male Eurasian lynx documented to mark at higher rates (Krofel et al. 2017). The use of scrape marking by temperate pumas (Logan and Sweanor 2010; Allen et al. 2014), combined with our work from the neotropics (this study), suggests that scraping is used by pumas across their range regardless of ecosystem and community composition. It is likely that we underestimated scent-marking rates of jaguars due to the lack of residual visual evidence left by spraying, rolling, and cheek rubbing, limiting our observations to opportunistic video records only (Allen et al. 2016b). Video placement was dictated by visual scrapes, thus likely biased towards puma marking sites.

As predicted, we detected only a subset of the jaguars and pumas as scent marking. Unlike Eurasian lynx, where all members of the population mark (Vogt et al. 2014), marking within large neotropical felid systems appears to be associated with a dominance hierarchy. Transient males of the population refrained from marking, at least on the trail system, potentially to avoid signaling their presence to resident males. We only documented marking by male transients when a female had recently been present on the trail, suggesting a trade-off between avoiding detection by residents versus opportunistic signaling to potential mates. This suggests males are constantly assessing, and reacting to, the presence and marks of competing resident males in an area.

Resident male pumas scraped more frequently with the presence of competitors and mates than in their absence. Individuals must partition time and energy resources to optimize activities, including hunting, searching for mates, and communicating (Pyke et al. 1977). It appears that pumas
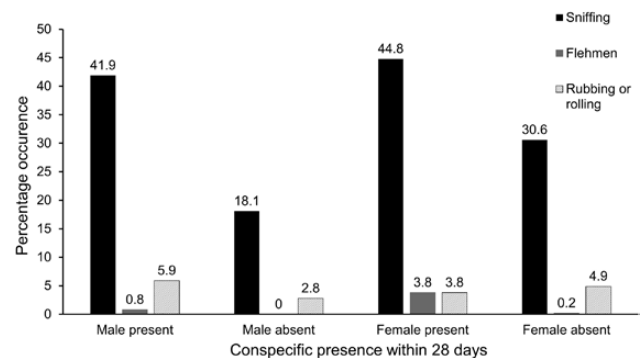

Fig. 4.—The proportion of visits at scrape clusters ($n = 30$) where pumas (*Puma concolor*) displayed scent-marking behaviors (scraping, rubbing or rolling, urinating on scrapes) and investigatory behaviors (sniffing, flehmen) in the Cockscomb Basin Wildlife Sanctuary, Belize. $n = 563$ male visits, 32 female visits, 536 resident male visits, and 27 transient male visits. Male pumas were more likely to mark than females ($d.f. = 1,595$, $P < 0.001$), and resident males more likely to mark than transients ($d.f. = 1,563$, $P < 0.01$).

Fig. 5.—The proportion of visits male pumas (*Puma concolor*) displayed sniffing, flehmen, and rubbing or rolling in response to the presence of conspecific males and females within the previous 28 days at scrape clusters ($n = 30$) in the Cockscomb Basin Wildlife Sanctuary, Belize. $n = 105$ female presence, 406 female absence, 389 male presence, and 177 male absence. Male pumas sniffed more frequently in response to male presence ($X^2_{1,566} = 12.4$, $P < 0.01$) and female presence ($X^2_{1,511} = 3.7$, $P < 0.05$).

modify their investment in scent-marking behavior depending on whether the mark is likely to be detected by a conspecific. In our study, female pumas visited the trail irregularly, in short bouts that likely corresponded to periods of estrus. Similar to Allen et al. (2015), we found that females associated with the resident males that scrape marked the most frequently, suggesting that females can distinguish individuals from their scrapes (Vogt et al. 2016). As such, male scraping may serve a functional role, increasing when females are in the local area, to signal that they are the local resident. Females may visit these locations to assess the signals, choosing males with the highest production of scrapes, which may act as an honest signal of mate quality (Allen et al. 2015). This may reduce the chance of infanticide of cubs as the sire is the local dominant (Allen et al. 2015). Allen et al. (2016c) found no increase in the scrape rate of male pumas in response to other males or females. However, they could not assess rates of scrape marking surrounding the video trap location. In our study, pumas marked along trail sections surveyed. As the frequency of scrape marking increased in the presence of conspecifics, we infer that scrape marking by pumas signals dominance in an area to competitors and potential mates.

Male pumas also returned sooner following the presence of conspecifics of both sexes (potential competitors and mates), similar to pumas in the temperate zone (Allen et al. 2016c). Likewise, the return interval of male jaguars decreased with the presence of other male jaguars, but not with the presence of females. However, unlike female pumas, which we detected on the trails irregularly, female jaguars were regularly present (albeit at a lower rate than males). Three of the nine detected female jaguars were repeatedly detected with dependents, thus we assume that they were unavailable for mating: two with three cubs < 1 year, and one with two juveniles > 1 year when first detected. It appears that while males respond to the presence of rival males by returning sooner to trails, this response may only occur for females when they are in estrus. Further study is needed to assess whether visitation by male jaguars is similarly influenced by presence of female jaguars when in estrus. The longer return interval of male jaguars compared to male pumas may be explained by the larger home ranges of jaguars compared to pumas in tropical rainforests (e.g., de la Torre et al. 2017).

We found evidence of smaller species investigating scent marks of co-existing larger species, but not the reverse. We documented one puma and two ocelots investigating the scent marks of jaguars, however, we found no evidence of the reverse situation. In Central-South America, jaguars are larger than pumas and considered the top predator (Iriarte et al. 1990; Harmsen et al. 2010a). Previous work in our study area has shown avoidance between jaguars and pumas, and the absence of pumas from areas frequently urine marked by jaguars (Harmsen et al. 2009, 2016). Potentially, pumas use the scent marks of jaguars, and ocelots use those of both pumas and jaguars, to avoid larger conspecifics. The lack of investigation by jaguars of puma or ocelot scent marks, and by pumas of ocelot scent marks, further suggests that within

this system larger species do not appear to actively search for, chase, or dispatch, smaller co-existing species. We also found evidence of non-felid mammals investigating puma and jaguar scent marks, in particular, collared peccaries, which are prey for both pumas and jaguars within the area (Foster et al. 2010). We documented a tayra rubbing its head and neck in the scat of a puma. This form of scent transference has been noted to be used by tayras at ocelot latrines in Costa Rica, and by gray foxes (*Urocyon cinereoargenteus*) at puma scrape clusters in North America (Allen et al. 2016a; King et al. 2016). It has been hypothesized that prey species, or smaller co-existing species, may investigate and use scent marks as an anti-predation strategy, as individuals are less likely to be attacked if they smell like a predator (Allen et al. 2016a; King et al. 2016). A greater range of species were detected investigating puma and jaguar scent marks, compared to ocelots, suggesting that scent marks of large felid species may play an important role within the local community.

LITERATURE CITED

ALLEN, M. L. 2014. The ecology and behaviour of pumas (*Puma concolor*) in Northern California, USA. Ph.D. thesis, Victoria University of Wellington, Wellington, New Zealand.

ALLEN, M. L., M. S. GUNTHER, AND C. C. WILMERS. 2016a. 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., H. U. WITTMER, P. HOUGHTALING, J. SMITH, L. M. ELBROCH, AND C. C. WILMERS. 2015. The role of scent marking in mate selection by female pumas (*Puma concolor*). PLoS ONE 10:e0139087.

ALLEN, M. L., H. U. WITTMER, E. SETIAWAN, S. JAFFE, AND A. J. MARSHALL. 2016b. Scent marking in Sunda clouded leopards (*Neofelis diardi*): novel observations close a key gap in understanding felid communication behaviours. Scientific Reports 6:35433.

ALLEN, M. L., H. U. WITTMER, AND C. C. WILMERS. 2014. Puma communication behaviours: understanding functional use and variation among sex and age classes. Behaviour 151:819–840.

ALLEN, M. L., V. YOVOVICH, AND C. C. WILMERS. 2016c. Evaluating the responses of a territorial solitary carnivore to potential mates and competitors. Scientific Reports 6:27257.

BAILEY, T. N. 1974. Social-organization in a bobcat population. Journal of Wildlife Management 38:435–446.

BAILEY, T. N. 1993. The African leopard: a study of the ecology and behavior of a solitary felid. Columbia University Press, New York.

BATES, D., M. MAECHLER, B. BOLKER, AND S. WALKER. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

BOLKER, B. M., ET AL. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

CRALL, J. P., C. V. STEWART, T. Y. BERGER-WOLF, D. I. RUBENSTEIN, AND S. R. SUNDARESAN. 2013. HotSpotter; patterned species instance recognition. Pp. 230–237 in Proceedings of the 2013 IEEE Workshop on Applications of Computer Vision (WACV), IEEE Computer Society.

DE LA TORRE, J. A., J. M. NUNEZ, AND R. A. MEDELLIN. 2017. Spatial requirements of jaguars and pumas in Southern Mexico. Mammalian Biology 84:52–60.

FOSTER, R. J., B. J. HARMSEN, B. VALDES, C. POMILLA, AND C. P. DONCASTER. 2010. The food habits of jaguars and pumas across a gradient of human disturbance. Journal of Zoology 208:309–318.

HARMSEN, B. J. 2006. The use of camera traps for estimating abundance and studying the ecology of jaguars (*Panthera onca*). Ph.D. thesis, University of Southampton, Southampton, United Kingdom.

HARMSEN, B. J., ET AL. 2017. Long term monitoring of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; implications for camera trap studies of carnivores. PLoS ONE 12:e0179505.

HARMSEN, B. J., R. J. FOSTER, S. M. GUTIERREZ, S. Y. MARIN, AND C. P. DONCASTER. 2010a. Scrape-marking behavior of jaguars (*Panthera onca*) and pumas (*Puma concolor*). Journal of Mammalogy 91:1225–1234.

HARMSEN, B. J., R. J. FOSTER, S. C. SILVER, L. E. T. OSTRO, AND C. P. DONCASTER. 2009. Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a neotropical forest. Journal of Mammalogy 90:612–620.

HARMSEN, B. J., R. J. FOSTER, S. SILVER, L. OSTRO, AND C. P. DONCASTER. 2010b. Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. Biotropica 42:126–133.

HARMSEN, B. J., E. SANCHEZ, AND R. J. FOSTER. 2016. Differential marking behaviour by sympatric felids in a Neotropical forest. Cat News 64:8–12.

HARMSEN, B. J., S. SILVER, L. OSTRO, AND C. P. DONCASTER. 2010c. The ecology of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize. Pp. 403–416 in The biology and conservation of wild felids (D. W. Macdonald and A. Loveridge, eds.). Oxford University Press, Oxford, United Kingdom.

HARRISON, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:e616.

IRIARTE, J. A., W. L. FRANKLIN, W. E. JOHNSON, AND K. H. REDFORD. 1990. Biographic variation of food habits and body size of the American puma. Oecologia 85:185–190.

KAMSTRA, J. 1996. Vegetation of the Cockscomb Basin. Pp. 35–67 in Cockscomb Basin Wildlife Sanctuary: its history, flora and fauna for visitors, teachers and scientists (J. Lumb, ed.). Angelus Press, Belize City, Belize.

KELLY, M. J., ET AL. 2008. Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. Journal of Mammalogy 89:408–418.

KING, T. W., R. SALOM-PEREZ, L. A. SHIPLEY, H. B. QUIGLEY, AND D. H. THORNTON. 2016. Ocelot latrines: communication centers for neotropical mammals. Journal of Mammalogy 98:106–113.

KORNER-NIEVERGELT, F., T. ROTH, S. V. FELTEN, J. GUELAT, B. ALMASI, AND P. KORNER-NIEVERGELT. 2015. Bayesian data analysis in ecology using linear models with R, BUGS and Stan. Elsevier, London, United Kingdom.

KROFEL, M., L. HOCEVAR, AND M. L. ALLEN. 2017. Does human infrastructure shape scent marking in a solitary felid? Mammalian Biology 87:36–39.

LOGAN, K. A., AND L. SWEANOR. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Covelo, California.

LOGAN, K. A., AND L. SWEANOR. 2010. Behavior and social organization of a solitary carnivore. University of Chicago Press, Chicago, Illinois.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging—selective review of theory and tests. Quarterly Review of Biology 52:137–154.

RABINOWITZ, A. R., AND B. G. NOTTINGHAM. 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. Journal of Zoology 210:149–159.

R CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

SCOGNAMILLO, D., I. E. MAXIT, M. SUNQUIST, AND J. POLISAR. 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan Llanos. Journal of Zoology 259:269–279.

SEIDENSTICKER, J. C., M. G. HORNOCKER, W. V. WILES, AND J. P. MESSICK. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35:1–60.

SMITH, J. L. D., C. MCDOUGAL, AND D. MIQUELLE. 1989. Scent marking in free-ranging tigers, *Panthera tigris*. Animal Behaviour 37:1–10.

SUNQUIST, M., AND F. SUNQUIST. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinois.

VOGT, K., S. BOOS, U. BREITENMOSER, AND M. KOLLIKER. 2016. Chemical composition of Eurasian lynx urine conveys information on reproductive state, individual identity, and urine age. Chemoecology 26:205–217.

VOGT, K., F. ZIMMERMANN, M. KOLLIKER, AND U. BREITENMOSER. 2014. Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. Behavioural Processes 106:98–106.

WECKEL, M., W. GIULIANO, AND S. SILVER. 2006. Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. Journal of Zoology 270:25–30.

ZEILEIS, A., AND T. HOTHORN. 2002. Diagnostic checking in regression relationships. R News 2:7–10.