

Scrape-marking behavior of jaguars (*Panthera onca*) and pumas (*Puma concolor*)

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Marking behaviors of jaguars (*Panthera onca*) and pumas (*Puma concolor*) were investigated by linking sign from transect surveys to species, sex, and individual detected by camera traps along trails in the Cockscomb Basin Wildlife Sanctuary, Belize. The most commonly encountered big-cat signs were scrape marks. These were produced by cats raking the ground with their feet. Scrapes were associated more strongly with presence of male pumas than with female pumas or jaguars of either sex. Scats found in scrapes were genotyped to species level and indicated that jaguars produced larger scrapes than pumas and that pumas were more likely to scrape with their hind feet than with front feet. Scrapes were spatially clustered along trails, indicating that individuals scrape in response to other scrapes in the same area. High scraping frequencies were not associated with the presence of specific individuals, suggesting that scrape-marking behavior does not signal dominance in this area. DOI: 10.1644/09-MAMM-A-416.1.

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Solitary carnivores must communicate indirectly with conspecifics to advertise social status, find mates, and regulate land tenure or foraging rights within an area (Gorman and Trowbridge 1989; Macdonald 1985; Sunquist and Sunquist 2002a). Solitary felids communicate indirectly by leaving olfactory signals for conspecifics. Detailed studies have been carried out on the marking behavior of easily observed felids, for example tigers (*Panthera tigris*—Smith et al. 1989), leopards (*Panthera pardus*—Bailey 1993), servals (*Leptailurus serval*—Geertsema 1985), feral domestic cats (*Felis catus*—Feldman 1994), and black-footed cats (*Felis nigripes*—Molteno et al. 1998).

Felids communicate over long distances either by calling (Kitchener 1991; Peters and Hast 1994; Peters and Wozencraft 1989; Sunquist and Sunquist 2002b) or by leaving (scent) markings (Asa 1993; Kitchener 1991; Mellen 1993; Sunquist and Sunquist 2002a). Markings are more durable and seem to be used almost universally by solitary felids (Kitchener 1991; Sunquist and Sunquist 2002a). Marking encompasses a number of behaviors; specifically, spraying urine, depositing feces, raking the ground with claws, rubbing against objects, and clawing trees (Kitchener 1991; Sunquist and Sunquist 2002a). Cats can identify a range of odors at relatively short

range, allowing them to decode olfactory signals left by conspecifics from scent glands, urine, and feces (Kitchener 1991; Macdonald 1985; Sunquist and Sunquist 2002a) and potentially assess age of the signal (de Boer 1977). Marking behavior in felids functions in territory demarcation (Gorman and Trowbridge 1989; Kitchener 1991; Smith et al. 1989; Sunquist and Sunquist 2002a) and mate attraction (Gorman and Trowbridge 1989; Kitchener 1991; Macdonald 1985; Molteno et al. 1998; Smith et al. 1989; Sunquist and Sunquist 2002a). Territorial marking can signal occupation of an area and thereby reduce conflict over resources of food or mates (Kitchener 1991; Logan and Sweanor 2009; Rabinowitz and Nottingham 1986; Smith et al. 1989; Sunquist and Sunquist 2002a). Often cats mark the boundary of their home range, particularly at contact zones with conspecifics, and more frequently after boundary changes or an influx of new conspecifics (Kitchener 1991; Laing and Lindzey 1993; Rabinowitz and Nottingham 1986; Smith et al. 1989; Sunquist and Sunquist 2002a). Female cats advertise their presence to



males during estrus by increased marking (Kitchener 1991; Molteno et al. 1998; Smith et al. 1989; Sunquist and Sunquist 2002a), and males mark more frequently when receptive females are in the area (Kitchener 1991; Smith et al. 1989; Sunquist and Sunquist 2002a).

Marking behaviors of elusive tropical forest felids remain understudied and generally unknown. For instance, little is known about the marking behavior of sympatric jaguars and pumas. The few published studies that refer to jaguar or puma marking behavior in the Neotropics indicate that marks most frequently observed by researchers are scrapes made by raking the paw through the dirt so as to create a scrape with a pile of dirt at one end (Crawshaw and Quigley 1991; Emmons 1987; Rabinowitz and Nottingham 1986; Schaller and Crawshaw 1980). This scraping action can deposit scent from glands in the feet (Kitchener 1991; Sunquist and Sunquist 2002a). Sometimes scats or urine are deposited in scrapes. Although scrapes on the ground are the most frequently encountered marks of jaguars and pumas in the Neotropics, nothing is known about how scrape-marking behavior and function might differ between these 2 cat species. Rabinowitz and Nottingham (1986) reported that jaguars in the Belizean rain forest frequently scraped on the ground and often marked these scrapes with scats on top of the raking, but pumas rarely scraped in this area. Scrape marks found in the rain forest of Manu, Peru, were assigned more often to pumas than to jaguars, with pumas scraping frequently and regularly and jaguars scraping infrequently and in clusters (Emmons 1987). However, no data were presented regarding frequency or periodicity of scrape-marking by either species. In the Pantanal, Brazil, scrape marks were rare and found only in association with pumas (Crawshaw and Quigley 1991; Schaller and Crawshaw 1980). In North America, beyond the geographic range of jaguars, pumas have been noted to scrape-mark frequently, particularly males (Logan and Sweenor 2009; Seidensticker et al. 1973).

Variation in scrape-marking behavior of jaguars and pumas across their range might reflect differences in social structure and abundance within and between the 2 cat species. Variation in land tenure has been observed across the geographic range of both species, varying from high levels of overlap between same-sex conspecifics (Cavalcanti and Gese 2009; Harmsen et al. 2009; Hopkins et al. 1986; Logan and Sweenor 2009; Rabinowitz and Nottingham 1986; Núñez et al. 2002; Seidensticker et al. 1973) to exclusive territoriality (Hopkins et al. 1986; Logan and Sweenor 2009; Schaller and Crawshaw 1980; Scognamillo et al. 2003; Seidensticker et al. 1973). Where these 2 solitary species coexist, evidence of interspecific avoidance can be found (Harmsen et al. 2009; Scognamillo et al. 2003), and it is possible that any such inter- and intraspecific avoidance could be facilitated via a signaling system such as scrape-marking.

We describe spatial and temporal patterns of scrape-marking and scat deposition by sympatric neotropical pumas (*Puma concolor*) and jaguars (*Panthera onca*) in Belize. These patterns were recognized by linking scrapes found in surveys

along forest trails to species, sex, and individual identified from camera-trap photographs and from genetic analysis of scats found within scrapes. In addition, we enumerate species-specific variation in scrape morphology to aid field identification of scrape marks to species level.

MATERIALS AND METHODS

The study was conducted in the Cockscomb Basin Wildlife Sanctuary in Belize, Central America. The Cockscomb Basin Wildlife Sanctuary forms part of the Maya Mountain forest block and encloses 425 km² of secondary, moist, broadleaf tropical forest at several stages of succession (Harmsen et al. 2010b; Rabinowitz and Nottingham 1986). The area was heavily logged until the 1980s and in 1990 was declared a wildlife sanctuary.

Long-term camera trap data has shown that Cockscomb Basin Wildlife Sanctuary has one of the highest known densities of jaguars in the Neotropics, ~9 adult jaguars/100 km² (Harmsen et al. 2010b; Silver et al. 2004). Puma density has not been estimated formally because many of the camera-trap photographs cannot be identified to individual with sufficient certainty due to the plain brown pelt color of pumas compared to the uniquely identifiable pattern of rosettes on jaguars (Harmsen 2006). Although the high frequency of photographic captures of pumas, equal to those of jaguars (Harmsen 2006), suggests a high density of pumas, short-term recognition of individuals over smaller spatial scales revealed fewer pumas compared to jaguars (Harmsen et al. 2010a). This finding agrees with other indices based on ratio of scat production, suggesting that jaguars are more abundant than pumas in the study area (Foster et al. 2010). Marking frequency likely will change with increasing density when more individuals will need to inform each other of their presence or avoid one another, and with decreasing density when individuals will have to increase their effort (higher marking frequency per individual) to raise their chances of communicating with other individuals. Land tenure habits also likely influence marking frequency, with populations that hold exclusive home ranges having different communication needs (mainly focused around boundaries) compared to species with higher spatial overlap of home ranges (marking taking place throughout the area). In our study area ranges of male jaguars overlap considerably (Harmsen et al. 2009; Rabinowitz and Nottingham 1986). Evidence that puma ranges overlap also exists, although the extent of such overlap is unknown (Harmsen et al. 2010a).

Scrape surveys.—Scrape surveys were conducted by 2 researchers walking slowly in parallel scanning for scrapes or other markings of large cats along the full length and width of designated trails. Trails were old logging roads (width 2.5–4.5 m) used exclusively by tourists for hiking with no vehicle traffic. Other trails (width 1.5–2 m) were established for scientific monitoring. Established trails were surveyed along their full length to include natural start and end features (e.g., rivers and mountain ridges) and so maximize the probability



FIG. 1.—Scrape made by a large cat in the Cockscomb Basin Wildlife Sanctuary in 2003 showing a raked-up pile of loose earth at the right and a partition in the middle of the scrape (pen indicates scale).

of encountering areas of home-range overlap or boundaries or both. Each transect was surveyed once per week (“weekly occasion”) to monitor spatial and temporal changes in scrape marks. Encountered scrapes were marked with small twigs and ribbons in nearby trees to prevent double counting on subsequent occasions. Between 2003 and 2004 scrapes were sought in 7 trail surveys of mean length ($\pm SD$) = 3.9 ± 2.8 km (range 2–10 km). One trail was surveyed twice, once in 2003 and once in 2004. The 8 surveys consisted of between 5 and 26 weekly occasions. Additionally, in 2007 a single 9-km trail was surveyed on 35 consecutive daily occasions sampled over an 8-week period.

A scrape was recognizable as raked ground with loose earth piled up at 1 end (claw marks were never visible). Two types of scrape were encountered, either 2 parallel rakings separated by a partitioning ridge of loose soil (double scrape; Fig. 1) or single rakings without partition (single scrape). As a working hypothesis we suggest that double rakings are created by raking along the ground with hind feet whereas single rakings are made by a single front foot (Fig. 2). A video trap, which was deployed once on 1 of the transect trails, filmed a puma scraping with a single front foot to produce what was identified subsequently as a single scrape.

The following variables were recorded when scrapes were encountered: single or double-raking scrape; Universal Transverse Mercator coordinates of each scrape location; scrape length excluding the earth pile and width measured from the outside edges of disturbed soil; and presence or absence of scat within scrape, with scats collected if present.

Scat collection and species identification.—Scats were collected during systematic scrape surveys. Scats frequently were found deposited in scrapes either on top of the pile of debris or on the open raked substrate. Scats were not covered as a result of scraping. We assumed that scats found in scrapes were deposited by the scraping individual because they were found only in new scrapes. Scats were never freshly deposited in previously encountered scrapes. Scats also were collected opportunistically during fieldwork between 2003 and 2006;



FIG. 2.—A resident male jaguar in Cockscomb Basin Wildlife Sanctuary in 2004 in the act of scraping on the ground with its hind feet to produce a double scrape.

although it was noted if scats were found in scrapes, no measurements were taken of these scrapes. All scats were dried with silica gel and stored at room temperature. DNA was extracted when possible using a QIAamp DNA Stool Mini Kit (Qiagen, Valencia, California) and genotyped to species. Foster et al. (2010) provided details on primer use and polymerase chain reaction analyses.

Camera trapping.—Camera stations were spaced at ~1-km intervals along survey trails and located to optimize capture probability of jaguars and pumas. Each station consisted of a pair of passive camera traps (Cam Trak South Ltd., Watkinsville, Georgia) positioned to photograph each side of the animal’s body, with continuous 24-h operation. An enforced 3-min delay between consecutive photographs reduced film wastage on multiple captures of herding species such as peccaries (Tayassuidae). Individual jaguars were identified from their unique pelt pattern (Silver et al. 2004). It also was possible to identify individual pumas visually from photographs over a temporal scale sufficient for this study by using scars, wounds, temporary swellings under the skin caused by botfly (*Dermatobia hominis*) larvae, and other identifiers such as residual juvenile markings (Harmsen 2006). Sex was determined by presence (or absence) of testes visible under the tail (Harmsen 2006).

Number of camera locations per trail ranged from 3 to 7, dependent on trail length. Photographs, hereafter referred to as “captures,” provided an index of number of cats per species, sex, and individual around each camera station. Two measures of jaguar and puma capture variables were calculated per camera location: total number of jaguar and puma captures, indicating activity of the 2 species at the location; and total number of jaguar and puma individuals identified, used as an approximate index of local abundance of each species at the location. Capture variables were partitioned further by sex. Jaguar and puma capture variables were calculated for the period between consecutive survey occasions, thereby matching cat presence within an area with number of scrapes produced during the same period. Because jaguars and pumas

do not always walk trails from start to finish (Harmsen et al. 2010a), photographic records reflect only cat presence for sections of trails. Therefore, only scrapes found within 1 km (either side of each camera location) were compared with jaguar and puma capture variables at those camera locations, which resulted in a constant survey length of 2 km of trail per camera station for analysis across all camera locations.

Data analysis.—Cat capture data from each camera location and scrape data within 1 km of each camera location were analyzed at 3 temporal scales: daily (2007 survey only), weekly, and over entire surveys, hereafter called daily, weekly, and total camera occasions. Pearson correlations (r) were used to estimate strength and direction of association between jaguar and puma capture variables and number of scrapes within 1 km of camera locations. A stepwise regression identified which of the capture variables best explained variance in scrape frequency. During survey occasions in which only 1 species of cat was detected by cameras, we assumed that scrapes around cameras were produced by that species. Data from these occasions were pooled for each species, and correlations were calculated for jaguar and puma capture variables and scraping frequency.

Spatial clustering of scrapes along trails was estimated from frequency distributions of distances separating neighboring scrapes. For 6 trails, sample sizes were sufficient to compare observed distributions to Poisson random distributions around the same mean using chi-square (χ^2) tests of association. This test was repeated for distances between closest neighboring scrapes produced over the 3 temporal scales of within-week, between weeks, and survey duration.

Scrape lengths and widths were tested for bimodal distributions, indicative of species differences. Student t -tests, assuming unequal variance, were used to determine differences between lengths and widths of double and single scrapes. The data were \log_{10} -transformed to approach normal distribution. For the subsample of scrapes with genotyped scats, length and width of jaguar and puma scrapes were compared with a Student's t -test assuming unequal variance. A chi-square (χ^2) test compared frequencies of jaguar and puma scrapes with single and double rakings with Yates' correction for continuity for chi-square analyses with 1 degree of freedom. The Mann-Whitney test (W) was used for an interspecific comparison of the number of scats found in scrapes within a survey occasion.

Statistical analyses were performed using Minitab version 14 (Minitab Ltd., Coventry, United Kingdom). The criterion for statistical significance for all analyses was $P < 0.05$.

RESULTS

Scrape activity and scat deposition varied between survey trails 0 scrapes and scats to as many as 9.4 and 0.4, respectively, per week per kilometer (Table 1). We detected no difference ($t_{18} = -1.67$, $P = 0.11$) in scrape activity between dry ($\bar{X} = 29.6$ scrapes ± 6.2 SE) and wet seasons ($\bar{X} = 44.1 \pm 6.1$ scrapes) over and above the large weekly

TABLE 1.—Mean numbers of scrapes and scats identified along 7 trails in Cockscomb Basin Wildlife Sanctuary between 2003 and 2005, surveyed on a weekly basis.

Transect (ID and year)	No. occasions (weeks)	Trail length (km)	Total scrapes (no.)	\bar{X} scrapes (scrapes week ⁻¹ km ⁻¹)	Scats in scrapes (no.)	Total scats (no.)	\bar{X} scats (scats week ⁻¹ km ⁻¹)	Minimum jaguar individuals (no.)	Minimum puma individuals (no.)
1. 2003	26	10.28	812	3.04	54	88	0.33	7♂, 2♀	4♂, 2♀
1. 2003 ^a	26	4.43	250	2.17	19	32	0.28	2♂, 1♀	3♂, 1♀
1. 2004	6	4.43	250	9.40	7	10	0.38	2♂, 0♀	1♂, 0♀
2. 2004	5	3.86	171	8.86	8	8	0.41	5♂, 1♀	1♂, 2♀
3. 2004	7	3.75	143	5.45	5	6	0.23	2♂, 3♀	1♂, 1♀
4. 2004	6	1.89	75	6.61	0	0	0.00	1♂, 1♀	1♂, 0♀
5. 2004	6	2.32	50	3.59	0	0	0.00	2♂, 0♀	2♂, 0♀
6. 2004	9	1.72	0	0.00	0	2	0.13	3♂, 1♀	1♂, 1♀
7. 2005	5	9.26	13	0.28	1	1	0.02	1♂, 1♀	1♂, 0♀

^a For comparison with the shorter but similar transect in 2004, the results for the 2003 survey are given for the subsample from the same stretch of transect as used in 2004.

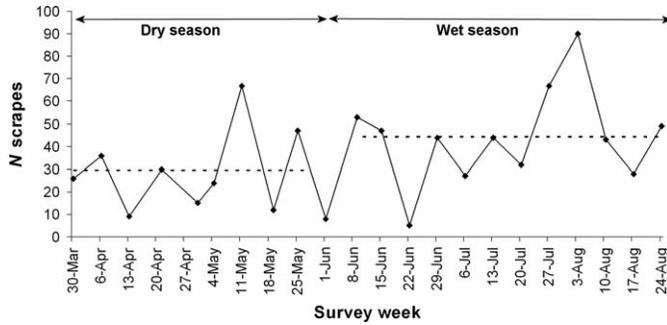


FIG. 3.—Number of new scrapes detected each week along Trail 1 (Table 1; 10.28 km long) during a scrape survey in Cockscomb Basin Wildlife Sanctuary in 2003. Dotted lines indicate mean number of scrapes found per season.

fluctuations, based on the longest survey conducted over 26 weeks between March and August 2003 (Fig. 3).

Scrape-marking activity and cat presence.—During the 2007 survey (Table 1) photo and scrape data were collected for 409 daily camera occasions. Stepwise regression on number of scrapes detected per day per camera location was positively correlated with total number of puma captures ($r = 0.12$, $n = 409$, $P < 0.05$), although this explained only 1.5% of the variation and was the only significant capture variable for either species. During this survey 53 scrapes were recorded within 1 km of camera locations; however, only 19 were directly linked with jaguar or puma captures on cameras. Thirty-four scraping events occurred without detection of cats on cameras, and jaguars and pumas were photographed on days when no scraping took place. Scrape-marking was associated more closely with pumas than jaguars: 12 of 23 puma captures were recorded with scrapes on the same day around the same camera locations, whereas only 7 of 37 jaguar captures were associated with scrapes ($\chi^2_1 = 5.79$, $P < 0.05$ with Yates' correction).

Across the 2003–2005 surveys 139 weekly camera occasions were analyzed for jaguar capture variables and for total captures of pumas. Because individual identification of pumas was not possible for 22 of the camera occasions, only 117 weekly camera occasions were available for analysis of male and female puma captures and for captures of individual pumas (79% of puma captures could be sexed and individually identified). Number of scrapes found each week around camera locations correlated more strongly with weekly puma captures at these camera locations than with weekly jaguar captures (Table 2). Within each species number of scrapes detected each week correlated most strongly with number of captures of male pumas each week and with captures of all jaguars (males plus females) each week (Table 2). However, stepwise regression indicated that variation in scrape activity was best explained by weekly capture rate of male pumas, and the weekly capture rate of jaguars had little additional explanatory value (Table 3).

Over entire survey periods (8 surveys, minimum duration 5 weeks, maximum duration 26 weeks; Table 1) total number of scrapes detected per camera location correlated positively

TABLE 2.—Pearson correlations (r) between the numbers of scrapes and jaguar and puma capture variables per camera location for a) weekly occasions ($n = 139$ for jaguar variables and total puma captures and 117 for the remaining puma variables), and b) pooled over entire survey periods ($n = 18$). All variables were \log_{10} -transformed to approximate normality. Correlations with $P < 0.05$ are in boldface type. All data were collected in Cockscomb Basin Wildlife Sanctuary between 2003 and 2005.

	Captures			Individuals		
	Total	Male	Female	Total	Male	Female
a) 1 week						
Jaguar	0.20	0.16	0.18	0.19	0.14	0.18
Puma	0.54	0.55	0.18	0.49	0.49	0.14
b) Complete						
Jaguar	0.67	0.69	0.24	0.81	0.83	0.47
Puma	0.72	0.73	0.43	0.68	0.67	0.65

with total number of jaguar captures and total number of puma captures at those locations (Table 2). Scrape activity correlated most strongly with number of individual male jaguars captured (Table 2) and accounted for 68% of the variation in scrape activity (Table 3). However, number of captures of male pumas explained an additional 9% of the variance in scrape activity (Table 3). Forcing male puma captures as the 1st input of the stepwise regression explained 50% of the variation, with number of male jaguar individuals explaining an additional 22% ($t_6 = 4.18$ and 3.84 for male puma captures and male jaguar individuals, respectively; $P < 0.01$ for both tests).

Male puma captures correlated positively with number of scrapes produced in weeks when jaguars were absent; conversely, neither jaguar captures nor jaguar individuals correlated with number of scrapes produced in weeks when pumas were absent (Table 4). We note, however, that sample size for jaguar-only weeks was less than half that for puma-only weeks. We found no evidence that high scrape activity was associated with capture of specific individuals or combinations of 2 individuals among either jaguars or pumas ($P > 0.10$ for all correlations; $r < 0.12$, $n = 139$ for weekly occasions and $r < 0.28$, $n = 18$ for data pooled over the entire survey period), indicating that scrape behavior was not restricted to resident individuals.

Spatial distribution of scrapes.—Frequency distributions of observed distances between neighboring scrapes differed markedly from random for all survey trails analyzed ($\chi^2_{22} > 50$, $P < 0.01$). The 2004 Trail 1 survey (Fig. 4) was representative of the other 5 surveys. The left skew and longer tail for all observed distributions relative to Poisson expectation indicates spatial clustering of scrapes. Most scrapes produced during any given week were sited within 0–10 m of each other (Fig. 4), indicating the cats respond to presence of a scrape by scraping. A similar pattern was found for distance between consecutive scrapes that were produced 1 week apart, although with less-pronounced clustering (Fig. 4). However, weekly sample sizes of scrapes varied (Fig. 3) such that some small-sample weeks were compared

TABLE 3.—Parameter estimates from stepwise regressions of number of scrapes as functions of jaguar and puma capture variables per camera location for a) weekly occasions ($n = 117$), and b) pooled over entire survey periods ($n = 18$). All variables were \log_{10} -transformed to approximate normality. Threshold type-I error for removing and entering variables was set at $\alpha = 0.15$. All data were collected in Cockscomb Basin Wildlife Sanctuary between 2003 and 2005.

a) 1 week			
Step	1	2	3
Constant	0.43	0.37	0.38
Puma male captures	0.92	0.93	0.92
t	7.17	7.42	7.46
P	0.00	0.00	0.00
Jaguar total captures		0.33	0.97
t		2.56	2.69
P		0.01	0.01
Jaguar male individuals			-0.80
t			-1.91
P			0.06
SD	0.29	0.28	0.28
r^2	0.30	0.33	0.35
b) Complete data set			
Step	1	2	3
Constant	0.97	0.74	0.65
Jaguar male individuals	0.82	0.58	0.51
t	4.65	3.71	1.81
P	0.00	0.00	0.09
Puma male captures		0.57	0.52
t		3.24	2.83
P		0.01	0.01
Jaguar total capture			0.26
t			1.56
P			0.14
SD	0.16	0.14	0.13
r^2	0.68	0.77	0.81

with large samples the following week, often inflating the distance between scrapes. A similar distribution of scrapes occurred over the entire survey period (Fig. 4), indicating that cats tended to scrape at particular locations along trails. Scrape clusters were distributed all along the trail, with the longest distance between scrape clusters being 386 m for a 10-km transect surveyed for 8 months.

Scrape dimension and form.—Frequency distributions of length and width of scrapes were unimodal for single and double scrapes, suggesting no species-specific scrape dimensions (Fig. 5). Almost twice as many single scrapes ($n = 824$) were found as double scrapes ($n = 495$). Although double scrapes were significantly shorter ($t_{1,227} = -9.56$, $P < 0.01$) and wider ($t_{1,238} = 4.86$, $P < 0.01$) than single scrapes, differences were relatively small (Fig. 5). Mean (SE range after \log_{10} back transformation) lengths and widths, respectively, of double scrapes were 23.1 (22.9–23.3) cm and 20.8 (20.7–21.0) cm, and of single scrapes, 25.7 (25.5–25.9) cm and 19.9 (19.7–20.3) cm.

Interspecific differences in scrape dimension and shape could be sought definitively only from scrapes with measured dimensions that also contained genotyped scats. Pumas were more likely than jaguars to produce double scrapes based on

TABLE 4.—Pearson correlations (r) between number of scrapes and jaguar and puma capture variables per camera location per week, in the absence of the other species. Data for jaguar scrapes come from the 19 occasions when only jaguars were detected on cameras, and data for puma scrapes come from the 48 occasions when only pumas were detected on cameras. All variables were \log_{10} -transformed to approximate a normal distribution. Correlations with $P < 0.05$ are in boldface type. All data were collected in Cockscomb Basin Wildlife Sanctuary between 2003 and 2005.

	Jaguar scrapes	Puma scrapes
No. captures		
Total	0.17	0.43
Male	0.03	0.42
Female	0.23	0.20
No. individuals		
Total	0.06	0.12
Male	-0.15	-0.07
Female	0.23	0.13

scats that were found in scrapes. Only 4 of 28 jaguar scats were found in double scrapes compared to 17 of 36 puma scats ($\chi^2_1 = 6.33$, $P < 0.05$ with Yates' correction). Small sample sizes limited comparison of dimensions between species to single scrapes (24 jaguar and 18 puma scrapes). Jaguars produced longer ($t_{36} = 6.66$, $P < 0.01$) and wider ($t_{38} = 2.26$, $P < 0.05$) single scrapes than pumas. Mean (SE range after \log_{10} back transformation) scrape lengths and widths, respectively, for jaguars were 36.8 (35.2–38.5) cm and 23.0 cm (22.1–24.0) cm, and for pumas, 23.7 cm (22.6–25.0) cm and 20.1 cm (19.2–21.0) cm.

Scats in scrapes.—The majority of scats were found in scrapes. Of the 350 scats collected opportunistically for which presence or absence of scrape was recorded, 265 were in scrapes. Scats that were not found in scrapes were either exposed on the trail without the cat manipulating ground cover or, less frequently (6 occasions), partially buried on trails.

Of 265 scats found in scrapes, 73 were genotyped to species level, of which 37 were attributed to jaguar and 36 to puma. Across the study area, a total of 513 scats was genotyped including the 73 from scrapes. Significantly more puma (median = 2, maximum = 6; $n = 14$) than jaguar (median = 1, maximum = 4; $n = 24$) scats were found in scrapes within a given survey occasion ($W = 332.5$, $P < 0.05$). During weeks when both jaguar and puma scrapes containing scats were found on the same trail, the numbers produced by jaguars and pumas were not related ($r = -0.31$, $n = 7$, $P = 0.50$). Remaining scats were collected opportunistically outside of survey periods by Cockscomb Basin Wildlife Sanctuary wardens without recording presence or absence of scrape. Of 513 scats, 371 were genotyped as jaguar and 141 as puma, suggesting that jaguars deposited at least 10% of scats in scrapes compared to pumas depositing at least 26% in scrapes ($\chi^2_1 = 18.98$, $P < 0.01$ with Yates' correction). Odor of cat urine was detected occasionally near trails but never directly within scrapes. New scrapes that were produced a day before were frequently encountered either opportunistically or during

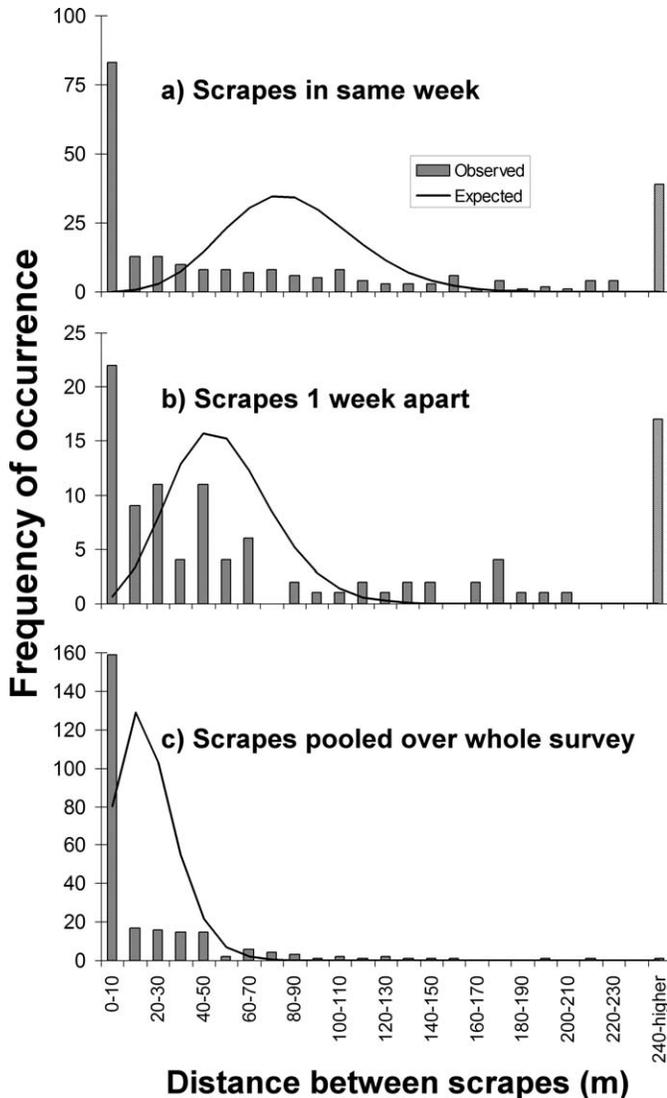


FIG. 4.—Frequency distributions of distances between neighboring scrapes along Trail 1 in Cockscomb Basin Wildlife Sanctuary in 2004 (see Table 1) compared with Poisson random expectation: a) scrapes produced during the same week (hatched bar = 240–1,136 m); b) scrapes separated by 1 week (hatched bar = 240–994 m); and c) all scrapes detected over the 6-week survey.

daily surveys. Fresh scats found in these scrapes often were detected by their odor from a distance of up to 10 m. All surveyors were familiar with the potent odor of large cat urine but on no occasion was the odor detected within a scrape. A rare photograph of a resident male jaguar spray-marking onto shrubby vegetation (Fig. 6) suggests that jaguars do not always spray on prominent solid objects.

DISCUSSION

Scrapes were the most frequently encountered signals made by large cats along forest trails in Cockscomb Basin Wildlife Sanctuary. However, it is premature to suggest that scrapes were the main source of communication within or between the 2 species. Calling or other olfactory signals (spray-marking or

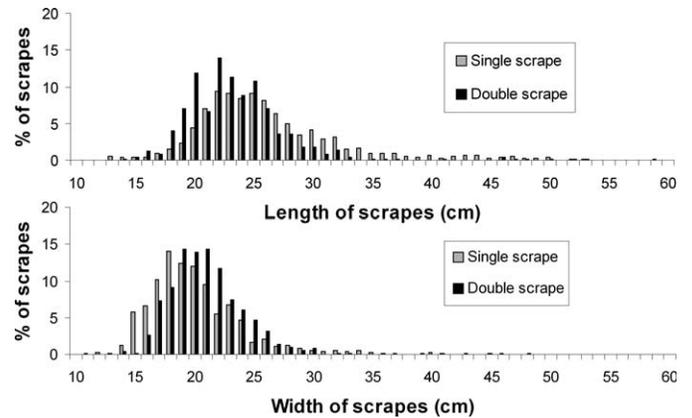


FIG. 5.—Relative frequency distribution of scrape lengths (upper panel) and scrape width (lower panel) from data pooled for all surveys carried out in Cockscomb Basin Wildlife Sanctuary between 2003 and 2005.

rubbing) could be important but are more difficult to detect or quantify by human observers. In contrast, scrape-marking frequencies of up to 9 scrapes per week per kilometer were recorded, with high spatial and temporal variation. Although the majority of scrapes lacked detectable sign of urine or scats, most scats found on trails were found in scrapes. However, we cannot conclude that most scats are deposited in scrapes because scats deposited elsewhere (off-trail or not in a scrape) are more cryptic and so probably undersampled. We found clear evidence that both cat species scrape-mark: scats genotyped as jaguar and as puma were found in scrapes, and camera and video traps recorded both cat species in the act of scraping.

We did not identify any morphological features of scrapes that allowed us to attribute scrapes to either species with certainty in the field in the absence of genetic data from scats. Scrapes containing scats seem to be of similar dimensions and shape to those without scats, suggesting that both fulfill a similar function. Genotyped scats from scrapes revealed that pumas were more likely to scrape with their hind feet and were responsible for smaller scrapes than jaguars. This size difference may be expected given that pumas tend to have narrower paws than jaguars (Reid 1997).

Analyses of the relationships between cat captures on camera and scrape production along trails at 3 temporal scales provided further evidence of the extent to which each species scrape-marked. At the broad temporal scale (on average more than 9 weeks) scrape production increased in the presence of jaguars and in the presence of pumas. The relationship between scrape production and each cat species was strongest, and of similar strength, for number of male puma visits (activity, as reflected by capture rate) and for number of individual male jaguars. Variation of survey duration did not influence this analysis because a similar analysis using only 5 weeks (shortest survey duration) yielded broadly similar results (Harmsen 2006). At the weekly scale scrape production also correlated positively with cat traffic, but in this case the correlation was much stronger for male puma capture rate



FIG. 6.—A resident male jaguar spray-marking secondary undergrowth at the edge of a trail in Cockscomb Basin Wildlife Sanctuary in 2007.

indicating a more direct relation between male puma than jaguar activity and scraping. At a fine temporal scale of daily surveys scrapes were detected within 1 km either side of a camera, but often no cats were photographed within the same 24-h period. This result indicated that insufficient cameras were deployed to detect the presence of cats on survey trails. Harmsen et al. (2010a) found that jaguars have a higher tendency than pumas to move on- and off-trail; therefore, they are more likely to escape detection by camera traps than pumas. The correlation between scrape production and jaguar activity was weaker than that between scrape production and puma activity, and this may be an artifact of the sampling method, which potentially undersampled jaguars. However, only 17% of jaguar captures during the daily survey coincided with scrapes produced on the same day, indicating a relatively low level of scrape-marking by jaguars when walking trails. With 52% of puma captures associated with scrapes produced on the same day, the sampling method is not the only explanation for a weak correlation between jaguar activity and scrape production; rather, it seems that jaguars scrape-mark less frequently than pumas. Also, scrape numbers and puma captures correlated positively during weeks when jaguars were not detected on cameras. In contrast, no significant correlation between scrape production and jaguar activity was found during weeks when pumas were absent. The higher scraping frequency by pumas is further supported by the higher rate at which we found puma scats in scrapes compared to jaguar scats. Our results are consistent with anecdotal data from other neotropical studies suggesting that jaguars scrape at a lower rate than pumas (Crawshaw and Quigley 1991; Emmons 1987; Schaller and Crawshaw 1980). The alternative explanation that jaguars scrape off-trail seems unlikely. We never encountered scrapes when walking off-trail in the forest or when cutting random transects through the forest; although jaguars had a higher tendency to leave the trails, they were far

more likely to be detected by cameras on- than off-trail (Harmsen et al. 2010a).

It is difficult to discern from our data whether scrapes function in interspecific communication. It is likely that both species have similar olfactory capabilities and are able to distinguish each other's signals. For example, Núñez et al. (2002) noted one occasion in which a puma responded to a jaguar scat by marking next to it. Puma scrapes containing scats were located ≥ 500 m from jaguar scrapes with scats produced during the same week, whereas they were occasionally found < 100 m (2–70 m) from other puma scrapes with scats. The numbers of jaguar and puma scrapes containing scats on the same trail were not related. Combined, these results suggest that interspecific countermarking is uncommon, and intraspecific countermarking is more common in pumas than in jaguars. Interspecific avoidance has been detected between jaguars and pumas in the Cockscomb Basin Wildlife Sanctuary (Harmsen et al. 2009). It is unknown whether this avoidance is mutual or one species is dominant over the other. Marking could play a role in facilitating this avoidance.

Where jaguars and pumas coexist jaguars tend to be larger (Iriarte et al. 1990). Intraguild competition could favor pumas that are subordinate or more wary than jaguars. One then might expect pumas to favor communicating with conspecifics in an inconspicuous manner when in the presence of a larger competitor such as a jaguar and, therefore, to use indirect signals such as scrape marks in preference to conspicuous signals such as calling, which could attract attention to their immediate location. Jaguar calls were common throughout the study area. In contrast, puma vocalizations were never heard (B. J. Harmsen and R. J. Foster, pers. obs.). The puma coexists with a number of other large carnivores in North America outside of the jaguar's range. Where its geographic range overlaps with that of wolves (*Canis lupus*), it actively avoids them (Akenson et al. 2005) and also is known to scrape-mark (Logan and Sweanor 2009; Seidensticker et al. 1973). Nothing is known about scrape-marking by pumas in Patagonia at the southern tip of their range where they are the largest carnivore. In the absence of larger competitors calling could be more common and scrape-marking less important. An alternative explanation could lie in the physiological difference between the 2 cat species. Jaguars belong to the *Panthera* lineage and can call more loudly than pumas, which are more closely related to the *Felis* lineage (Yu and Zhang 2005). Scrape-marking by pumas might have evolved as a mechanism of indirect signaling, especially applicable to dense forests where low-amplitude calls are impeded.

We found no evidence that scraping was associated with presence of a specific individual or few individuals of either species, suggesting that this behavior is not limited to dominant or resident individuals. Scrape production increased with male puma traffic along trails, regardless of the number of individual pumas using the trail, and we infer that scraping by pumas can function to signal temporary presence rather than demarcating a territory. We found no evidence that

scraping increased with presence of females of either species. Our findings are consistent with data from temperate regions of North America showing that male pumas are most frequently responsible for scrapes, which females subsequently use for assessing status of potential mates without countermarking (Logan and Sweaner 2009). Although puma presence explained much of the variation in scraping, remaining variation that could be explained by jaguar captures seemed to indicate a stronger relation with number of individuals than with overall activity. This finding would mean that, unlike pumas, jaguars are more likely to scrape when other jaguars are in the area. The higher abundance of jaguars compared to pumas could be responsible for the difference in scrape behavior and function, with jaguars reacting to the presence of conspecifics as competitors—for example, to regulate land use—and pumas constantly having to signal their presence to communicate with conspecifics in a low-density population. We acknowledge that the potentially lower reliability of individual puma recognition could underemphasize the influence of local abundance (number of individuals) compared to activity (number of captures), which is the more reliable indicator of puma abundance. We remain confident, however, that puma individuals included in this analysis had enough identifiable features for individual identification.

Scrapes were spatially clustered, most commonly within 0–10 m of each other regardless of the time interval between production (0–26 weeks). Spatial clustering indicates that cats respond to scrapes by scraping, either remarking their own scrapes at particular locations or marking near scrapes left by other individuals (conspecifics or different cat species). Although scrapes were found in clusters, clusters were found along the full length of survey trails. We found no distinct zones indicative of scraping only at territory boundaries, as reported by Smith et al. (1989) and Kitchener (1991). Maximum separation between scrapes was only 386 m for a 10-km transect. We infer that although cats scrape near existing scrapes, no specific areas could be classified as contact zones between territories. The high variation in scrape production between weeks and years in the same location suggests a marking system not based on exclusive territoriality. These findings concur with camera-trap and telemetry studies conducted in Cockscomb Basin Wildlife Sanctuary, which indicated substantial overlap in ranges of multiple male jaguars and of multiple male pumas (Harmsen et al. 2009; Harmsen et al. 2010a; Rabinowitz and Nottingham 1986).

The role of urine needs further study, because our methods were inadequate for reliable quantification. We are confident that a large proportion of scrapes were without urine, but additional studies using better methods (e.g., black light searches at night) might yield the appropriate quantitative data. Marking behavior conceivably depends on population density, with a function of advertising presence being most prominent at low densities and a warning response function prevailing at higher densities. Such density dependence might explain the more frequent scraping by the less-abundant puma

correlating with puma captures, and the correlation of scraping by the more-abundant jaguar with numbers of individuals. To associate density with species more accurately additional data are needed on both species from areas at different densities.

RESUMEN

Comportamiento de marcaje de jaguares (*Panthera onca*) y pumas (*Puma concolor*) fueron investigados interrelacionando marcas encontradas en transectos a lo largo de senderos en el Cockscomb Basin Wildlife Sanctuary, Belize, con especies, sexo, e individuo detectados por foto trampeo. Las marcas más comunes encontradas de los felinos grandes fueron arañazos en el suelo. Estos fueron creados por los felinos al arañar el suelo con las patas. Los arañazos fueron más fuertemente relacionados con la presencia de pumas macho que con pumas hembra o jaguares de ambos sexos. Heces encontradas en arañazos fueron identificados por genotipo a nivel de especie lo cual indica que los jaguares producen arañazos más grande que los pumas, y más probable que los pumas marquen usando las patas traseras que con las del frente. Arañazos fueron encontrados espacialmente agrupados a lo largo de los senderos lo cual indica que individuos arañan en respuesta a otros arañazos en el mismo área. Frecuencia muy alta de arañazos no fueron asociadas con la presencia de individuos en específico, lo cual sugiere que el comportamiento de marcaje por arañazos no señala dominancia en el área.

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