



Puma communication behaviours: understanding functional use and variation among sex and age classes

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Abstract

Intraspecific communication for mate selection sometimes varies between sexes based on different evolutionary life history patterns. Solitary felids use communication for territorial defence and location of mates, for which they use scent-marking behaviours including scraping, urine spraying, body rubbing, caterwauling, cheek rubbing, and the flehmen response, but these behaviours are not well understood in pumas (*Puma concolor*). We used motion-triggered video cameras to document the use of communication behaviours by male and female pumas, and used a series of experimental treatments to determine the mechanisms and importance of visual and olfactory cues in puma scrapes. We found that pumas use the physical scrape to locate communications, and then use urine to convey and interpret the communication itself. We also found significant differences among puma age and sex classes in the proportion of use and duration of time behaviours were displayed. Mature males spent significantly longer durations ($\bar{x} = 22.1$ s) on producing behaviours (scraping, body rubbing, and caterwauling behaviours) than mature females ($\bar{x} = 3.3$ s), and males used scraping (78.5%) and body rubbing (12.4%) behaviours at a higher proportion of visits than females (13.6 and 2.7%, respectively). Mature females spent significantly longer durations ($\bar{x} = 30.4$ s) on consuming behaviours (investigating and flehmen response behaviours) than mature males ($\bar{x} = 13.7$ s), and females used flehmen response (30.6%) and caterwauling (9.3%) behaviours at a higher proportion of visits than mature males (6.5% flehmen and 0.4% caterwauling). Male reproductive strategy appears based on advertisement for possible mates, while female reproductive strategy appears based on assessment of possible mates. The use of communication behaviours also appears to develop with age, as immature pumas rarely visited and acted as non-participants in communication behaviours.

Keywords

behaviour, communication, puma, *Puma concolor*, reproduction strategy, scent-marking, scraping, sexual dimorphism.

1. Introduction

Communication, defined as the transfer of information by an individual or group to another individual or group (Gundersen, 1976), is an important component to understanding functions and evolution of animal behaviour. Intraspecific communication is important because it is one of the key aspects of social organization, and has been shown to directly affect individual fitness (Breed & Moore, 2011; Davies et al., 2012). The use of intraspecific communication for mate selection is often dramatically different between sexes, and based on different evolutionary reproductive strategies (Logan & Swenor, 2001; Breed & Moore, 2011; Davies et al., 2012). How drastic the sexually dimorphic differences in communication are varies among taxonomic groups and depends upon life history patterns (Verberne & Leyhausen, 1976; Mellen, 1993).

Many solitary felids exhibit sexually dimorphic traits in both communication and life history patterns, including their use of scent-marking and courtship behaviours (Logan & Swenor, 2001; Sunquist & Sunquist, 2002; Harmsen et al., 2010). Solitary felids have spatially dispersed populations and intraspecific communication is most frequently via indirect signals through scent-marking (Seidensticker et al., 1973; Smith et al., 1989; Bailey, 1993; Logan & Swenor, 2001, 2010; Harmsen et al., 2010). Due to this, their most frequent forms of communication are visual and olfactory signals, along with less common auditory and tactile signals (Bailey, 1993; Logan & Swenor, 2001, 2010; Sunquist & Sunquist, 2002). In many species males create scent-marks more often than females (Seidensticker et al., 1973; Logan & Swenor, 2001, 2010; Sunquist & Sunquist, 2002; Harmsen et al., 2010). Mellen (1993) documented a variety of communication behaviours in captive felids, including scraping, urine spraying, and body rubbing (see Table 2 for definitions), with sexually dimorphic tendencies in many species. However, the differences in the use of communication behaviours between sexes and the mechanisms behind mate selection among different felid species are understudied.

Though many aspects of puma (*Puma concolor*) behaviour are similar to other felids (Sunquist & Sunquist, 2002), they differ in their distribution pattern and reproductive behaviours. Most large felids inhabit equatorial regions, and breed throughout the year (e.g., cheetahs, *Acinonyx jubatus*, and jaguars, *Panthera onca*), while most felids that inhabit northern latitudes (i.e., Eurasian Lynx, *Lynx lynx*, Bobcat, *L. rufus*, Canada Lynx, *L.*

canadensis, European Wildcat, *Felis silvestris*) are smaller and have very short breeding periods during the late winter or early spring (Sunquist & Sunquist, 2002). Pumas range extends high into northern and southern latitudes in the Americas (Sunquist & Sunquist, 2002), and unlike most other felids in northern latitudes, they mate throughout the year (though there are other exceptions, e.g., tiger, *Panthera tigris*, and leopard, *Panthera pardus*). Logan & Sweanor (2001, 2010) hypothesized that the result of pumas being spatially dispersed and reproductive behaviours occurring throughout the year, has led to sexually dimorphic evolutionary reproductive strategies, including the avoidance of males by females when they are raising young. If so, these strategies would extend to their use of communication behaviours, which are important to the success of the strategy.

Pumas use indirect methods of scent-marking and other behaviours to communicate with conspecifics. The most common form of puma communication is scraping (Currier, 1983; Logan & Sweanor, 2001), which is a combination of visual and olfactory signals. Scrapes are depressions in the ground excavated by the puma's hind feet, most commonly comprised of leaf litter or duff, and usually accompanied by urine and occasionally faeces (Seidensticker et al., 1973; Currier, 1983; Logan & Sweanor, 2001; Elbroch, 2003). Currently, the relative importance of visual and olfactory components in scrape communications is unknown (Logan & Sweanor, 2010). Scrapes are regularly created along territorial boundaries or prominent travel-ways (Seidensticker et al., 1983; Logan & Sweanor, 2010), and are thought to be made primarily by adult males and less often or not at all by females or sub-adult males (Seidensticker et al., 1983; Logan & Sweanor, 2001, 2010; Harmsen et al., 2010). Other communication behaviours used by pumas in conjunction with scraping behaviour include caterwauling, cheek rubbing, and the flehmen response (Verberne & Leyhausen, 1976; Mellen, 1993; Harmsen et al., 2010; McBride & McBride, 2010; McBride & Sensor, 2012).

We initiated a study to determine intraspecific functions of scraping behaviour based on videos recorded by motion-triggered cameras placed at known scent-marking areas of pumas in California. Our first objective was using an experimental treatment design to determine the mechanisms and importance of different components of scrapes. We hypothesized that visual cues (the physical scrape) would be used to locate the scrape, while olfactory cues (the urine) would be used to transmit signals (hypotheses for each treatment noted in Table 1). Our second objective was to determine

Table 1.

Design and hypotheses for the experimental treatment sets.

Set	Design				Hypotheses		
	0	a	b	ab	First detection	Investigation rate	Investigation duration
0-a	+	+	-	-	$0 < a$	$0 < a$	$0 < a$
0-b	+	-	+	-	$0 < b$	$0 < b$	$0 < b$
0-ab	+	-	-	+	$0 < ab$	$0 < ab$	$0 < ab$
a-b	-	+	+	-	$a < b$	$a < b$	$a > b$
a-ab	-	+	-	+	$a < ab$	$a < ab$	$a = ab$
b-ab	-	-	+	+	$b = ab$	$b = ab$	$b < ab$

The design shows the composition of the variables present at each experimental treatment set. The hypotheses show how we expected variables to perform against each other, including first detection rates, investigation rates, and investigation duration. 0, control (nothing); a, puma urine; b, physical scrape; ab, puma urine and physical scrape.

whether scraping and associated behaviours were used in different proportions or durations by sex and age classes, based on the hypothesis of Logan & Sweanor (2001, 2010) that male and female pumas have evolutionarily different breeding strategies. We first set out to determine if differences occurred in the proportion of use of communication behaviours among puma sex and age classes (hypotheses for each behaviour noted in Table 2). We next set out to determine if puma sex and age classes spent different durations of time displaying producing (scraping, body rubbing, and caterwauling behaviours) and consuming (investigating and flehmen response behaviours) behaviours at scrapes (hypotheses noted in Table 2).

2. Materials and methods

2.1. Study area

We conducted our study in a 17 000 km² study area in the Santa Cruz Mountains, including parts of Santa Cruz, San Mateo, and Santa Clara counties of California (Figure 1). The puma population is not hunted and was considered to be at high density, with most mortality caused by humans (e.g., killed due to livestock depredations or through vehicle collisions). The study area was bounded by the Pacific Ocean to the west, the cities of San Francisco and San Jose to the north, and Highway 101 to the east. A major highway (Highway 17) bisects the study area. Major habitat types in the study area

Table 2. Definitions of puma communication behaviours, and our hypotheses regarding differences in the proportion and duration of communication behaviours among puma sex and age classes.

Behaviour	Definition	Hypothesis	Rationale
Scraping	Where the puma scraped in substrate with their hind feet and sometimes urinated and/or defecated on the scrape	Mature males will scrape at higher rates than other classes	Due to female mate choice and male territoriality, we expect males to advertise their fitness most often, and expect females to advertise only when in oestrus
Olfactory investigation	Where the puma is using its olfactory sense to investigate cues and signals, noted by the pumas nose within 15 cm of a scrape or other cue	Investigation rates will be similar among all three classes	Because scraping behaviour is the most common form of intraspecific communication, we would expect all classes of pumas to be investigating at equal rates
Body rubbing	Where the puma rubs its cheek or shoulder on the ground, a stump, or tree branch, or rolls back and forth on the ground	Mature males will body rub at higher rates than other classes	Due to female mate choice and male territoriality, we expect males to advertise their presence most frequently
Caterwauling	Where the puma gives a loud and reverberating call characterized by multiple changes in pitch	Mature females will caterwaul at higher rates than other classes	Females are thought to caterwaul to attract prospective mates when they are in oestrus; this behaviour has not been recorded in males

Table 2.
(Continued.)

Behaviour	Definition	Hypothesis	Rationale
Flehmen response	Where the puma picked up its head and curled back its upper lip, sometimes arching its neck backwards, in order to expose its vomeronasal organ	Mature female flehmen response rates will be higher than other classes	Because the flehmen response is used to assess potential mates, females will use flehmen response at higher rates based on classic female choice theory
Producing	The communication behaviours of scraping, body rubbing, and caterwauling	Mature males would spend longer durations on producing behaviours than other classes	If male strategy is based on advertisement they would be motivated to spend longer durations producing signals for prospective mates to find than other classes
Consuming	The communication behaviours of investigating and flehmen responses	Mature females would spend longer durations on consuming behaviours than other classes	If female puma strategy is based on assessment they would be motivated to assess the status of all possible mates and spend longer durations consuming signals than other classes

Puma classes include mature males and females (≥ 2.5 years) and immature pumas (< 2.5 years). The behaviour hypotheses regard the proportion of visits where pumas of each class would exhibit the five behaviours, while the producing and consuming hypotheses regard the differences in duration between puma classes.

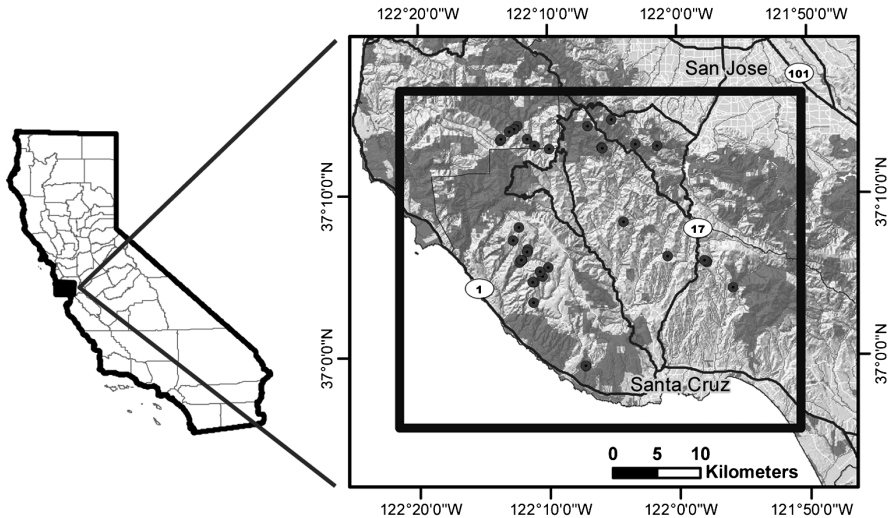


Figure 1. A map of the study area, which included areas in Santa Cruz, San Mateo and Santa Clara Counties in California. The study area is outlined by the thick black line, within the greater context of major highways and the cities of Santa Cruz and San Jose, and the location of each camera is noted.

changed with distance from the coast, and included: coastal scrub, coastal oak woodland, annual grassland, redwood (*Sequoia sempervirens*), montane hardwood–conifer, montane riparian, mixed chaparral, montane chaparral, montane hardwood, ponderosa pine (*Pinus ponderosa*), eucalyptus, valley foothill riparian, and valley oak woodland (Mayer & Laundenslayer, 1988). Elevation ranged from sea level to 1155 m, and the climate is best described as mild Mediterranean. Historical average daily high temperatures ranged from 15.5–24.4°C and average daily low temperatures ranged from 3.9–11.1°C. The annual rainfall varied from 58–121 cm, the majority of which occurred from November to April (Wilmers et al., 2013).

2.2. Definitions and field methods

Among puma biologists there has arisen a unique and dispersed terminology regarding scraping behaviour; for the purposes of this study, we differentiated between what we termed ‘individual scrapes’ and ‘community scrapes’. Individual scrapes are the outcome of scraping behaviour — at its most simple, a scrape. Community scrapes are defined as scrape areas used regularly to communicate with conspecifics, and are therefore used by more than one puma. These areas were previously described by Logan & Sweanor (2001)

as shared scrape sites, and by Harmsen et al. (2010) as scrape clusters. Community scrapes were identified by an abundance of scrapes in a concentrated area (roughly ≥ 3 scrapes within 9 m^2 , though this can vary depending on substrate and visitation), which had no association with either kill or bedding sites.

Our first step was to find and document individual and community scrapes. We initially found community scrapes by searching dominant landscape features, areas commonly used by pumas, and by following puma tracks across the landscape. As the study progressed, we used a modification of a custom program we had developed for identifying kill sites through GPS data, and used it to locate potential community scrapes based on clusters of GPS locations more than 7 days apart from each other in time (Wilmers et al., 2013). We used the data from our first 9 males (ages 2.5–9 years) and then visited these sites and searched the area for the presence of scrapes. We took measurements of width and length of individual scrapes and accompanying tracks to confirm the scrapes were created by pumas (Elbroch, 2003). We set up motion-triggered video cameras with infrared flash (Bushnell TrophyCam, Overland Park, KS, USA) at 26 spatially independent community scrapes for the experimental treatments (see below), with each community scrape being at least, 200 m from each other. We then added additional cameras for monitoring communication behaviours, though not always spatially independent, for a total of 45 community scrapes monitored. The cameras were programmed for maximum recording and viewing, with a set-up to record a 60 s video every time motion was detected with a 1 s delay before triggering again.

We concurrently captured 36 pumas from 2008–2012 using trailing hounds, cage traps, or leg-hold snares. Upon capture pumas were anesthetized with Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA). Once anesthetized, pumas were sexed, weighed and measured, and then fit with an ear tag and a combined GPS/radio telemetry collar (Vectronics Aerospace, Berlin, Germany). The Independent Animal Care and Use Committee at the University of California, Santa Cruz approved all animal-handling procedures. When possible, individual collared pumas detected on cameras were identified by unique collar identifiers and/or ear tags, while pumas without collars were identified by the spotting patterns on the inside of the upper leg and other unique features including scarring, kinks in their tail, and old injuries (Kelly et al., 2008). During captures age was deter-

mined through measurements of gum line recession (Laundré et al., 2000) for each individual. When possible, we determined the sex and age classes (mature > 2.5 years old, immature < 2.5 years old) for individuals without collars through the position of genitals and external physical characteristics (Ashman et al., 1983; Currier, 1983).

2.3. *Experimental treatments design*

After community scrapes were located, we created a series of experimental treatments at 26 community scrapes, to determine the roles of the visual and olfactory cues in puma individual scrapes. We created the experimental treatments based on a crossover design (Table 1), and distributed the paired experimental treatments in a random design. Each community scrape was given a numeric label, and each treatment variable pair was assigned to a numbered community scrape, before rotating to the next sequential number the following month. Each community scrape had a most common route of travel for the pumas (though the pumas were as likely to enter or exit from either direction). We determined the most likely route of travel, and created the treatment variables on either side of this route to allow equal probability of detection. This was accounted for in the random design with each treatment variable pair switching sides (from left to right from the cameras perspective) in the sequential pairs. The experimental treatments involved 6 different pairs of scrape variables; the designs each involve the presence or absence of male puma urine (a), a physical scrape (b) and control (0). We used the first visit by a puma to each experimental treatment set as our samples for analyses.

All experimental treatments were created by the same person to control for reliability and variation. Physical scrape components were created by hand using scent-free latex gloves, and we administered 0.5 ml of puma urine from a glass eyedropper for the urine components. For the control, we did not use either a physical scrape or urine, and instead patted the ground with gloved hands three times to control for human presence or any novel scents created at the community scrape. We purchased the un-neutered male puma urine from a captive facility (InHeatScents, Troy, AL, USA) where they collected the urine from live pumas. The set of experimental treatments were monitored for 3–4 weeks, and then at the end of the monitoring period we raked the community scrape and created the new set of experimental treatments based on our random design.

We viewed each video for puma activity and reaction to the experimental treatments, and quantified 3 olfaction responses: first investigation, investigation rate, and the investigation duration. We defined olfactory investigation as when a puma was actively sniffing one of the components of the experimental treatment with its nose within 15 cm of it. We defined first investigation as the treatment variable which the puma olfactory investigated first during its visit. Investigation rate was determined as the proportion of each treatment variable which was olfactory investigated by the pumas during visits. We determined the investigation duration by recording the duration of time the puma olfactory investigated each of the experimental treatments.

2.4. Communication behaviour design

We attempted to determine whether scraping and associated behaviours were used differently by pumas of different sex and age classes. We first removed any videos where pumas were reacting to the experimental scrape treatments we had created, in case our experiments caused changes in the puma's behaviour, and then analysed the remaining videos of puma visits. When possible, we identified the individual puma (either collared pumas or pumas without collars with distinctive markings), and categorized the puma as mature male, mature female, immature male, or immature female, with immature pumas either independent or traveling with their mother. We censored any videos where we were unable to determine the class of pumas without collars. We watched each video which recorded a puma visiting a community scrape from February 2010–December 2012, and quantified the different behaviours it displayed while at the community scrape. In each video we recorded the duration of the overall visit to the closest second; and we then noted the occurrence of 5 behaviours and recorded the duration of each behaviour to the closest second. The behaviours included: scraping, olfactory investigation, body rubbing, flehmen response, and caterwauling (with definitions in Table 2). We then grouped scraping, body rubbing, and caterwauling into the category of producing behaviours, and grouped olfactory investigation and flehmen responses into consuming behaviours.

2.5. Statistical analyses

We used program R version 3.0.0 (R Core Team, 2013) for all statistical analyses. Following R guidelines (R Core Team, 2013), we cite any associated packages used in the analyses. Before performing statistical analyses we tested each continuous variable data set for normality with a Shapiro–Wilk

test and for variance equality with a Levene's test (Sokal & Rohlf, 1987). In each analysis, we considered $p < 0.05$ significant.

2.5.1. Experimental treatment statistical analyses

We analysed the experimental treatments based on the paired design of the experiments, with each statistical test between the variables present at an experimental treatment set (Table 1). We tested three different sets of hypotheses (Table 1) for each experimental treatment: which variable was investigated first, the investigation rate for each variable, and the duration of time each variable was investigated. For example, we first tested the experimental treatment set of puma urine versus the control, and tested for differences in the two treatment variables in first investigation, investigation rate, duration of investigation (using the analyses below), and then progressed through each experimental treatment set in turn.

For first investigation, we first removed samples where no variable was investigated, and then used a binomial probability test (Sokal & Rohlf, 1987) to determine if the treatment variables were different in their rate of being investigated first. For investigation rate, we used a z -test of proportions between two populations (Sokal & Rohlf, 1987) to determine if treatment variables were investigated in a different proportion of puma visits. For duration of investigation, because of a lack of homoscedasticity we used a two-way Student's t -test with unequal variances (Sokal & Rohlf, 1987) to test for differences between the treatment variables. After testing our hypotheses, we created post-hoc effect sizes based on Cohen's d score (Cohen, 1992) for values with significant differences, and we considered scores of 0.20 small effects, 0.50 medium effects, and 0.80 large effects (Cohen, 1992).

2.5.2. Communication behaviours statistical analyses

We used a series of analyses to determine if pumas of different sex and age classes varied in their use of communication behaviours at community scrape sites (Table 2). To account for malfunctions of cameras and ensure we recorded the majority of a visit we removed samples with substandard quality and videos where we recorded less than 8 s of a puma visit. We initially had 5 puma age and sex classes: mature males ($N = 535$), mature females alone ($N = 152$), mature females with cubs ($N = 14$), immature males ($N = 40$), and immature females ($N = 11$). We first did pre-tests for each behaviour, first testing for differences between females with cubs against females without cubs, and then testing immature males against immature females. We did not find any statistical significant differences in the pre-tests, and we there-

fore pooled the visits for females with and without cubs, and also pooled all immature pumas together. In each analysis we then tested among 3 puma classes: mature males, mature females, and immature pumas. Because the majority of visits were by mature male pumas, we only used the first 10 visits by each individual mature male puma to each monitored community scrape in order to control for the large sample size of males in comparison to females and immature pumas.

First, we tested for differences in the duration of visits to community scrapes among each puma class (mature males, mature females, and immature pumas). We determined duration of time for each visit to the closest second, and then used a mixed-model Analysis of Variance (ANOVA) to test for differences among puma classes using the nlme package (Pinheiro et al., 2013). We used the visit duration as our dependent variable, puma class as a fixed independent variable, and known individual pumas as a random independent variable (to account for the variable number of samples among individual pumas).

Second, we tested if puma classes displayed each communication behaviour (scraping, olfactory investigation, caterwauling, flehmen response and body rubbing) in a different proportion of visits using a chi-square test (Sokal & Rohlf, 1987). In some cases, because of very low proportions of behaviours, we used a Fisher's exact test instead of a chi-square test (Sokal & Rohlf, 1987); in these cases we just report the degrees of freedom and *p*-values. We then calculated post hoc effect sizes for behaviours with significant statistical differences by calculating *phi* coefficients (Yule, 1912), using the vcd package (Meyer et al., 2013), and we considered scores of 0.10 small effects, 0.30 medium effects, and 0.50 large effects (Cohen, 1992).

Third, we determined the duration of time pumas displayed each type of behaviour during visits to the closest second, and then tested for differences in the duration of time puma classes spent displaying producing and consuming behaviours (Table 2). Due to the lack of linearity and homoscedasticity, we performed a logarithmic transformation (Sokal & Rohlf, 1987) in order to meet the assumptions of the ANOVA. We then used two mixed-model ANOVAs in the nlme package (Pinheiro et al., 2013), with the first model used for producing behaviours and the second model used for consuming behaviours. We used the duration spent on the behaviour during a visit as our dependent variable, puma class as a fixed independent variable, and known individual pumas as a random independent variable (to account for the variable number of samples among individual pumas).

3. Results

3.1. Experimental treatments

Our analyses revealed that when compared to the control the puma urine was not investigated first more frequently, nor investigated at a higher rate, or investigated for longer durations of time (Tables 3 and 4). In contrast, when compared to the control, the physical scrape and the physical scrape with urine were investigated first more frequently ($p_b = 0.0414$, $p_{ab} = 0.0015$), investigated at a higher rate ($p_b = 0.0011$, $p_{ab} = 0.0004$), and investigated for longer durations of time ($p_b = 0.0004$, $d_b = 1.29$, $p_{ab} < 0.0001$, $d_{ab} = 1.74$). When compared to the puma urine, the physical scrape and the physical scrape with urine were investigated first more often ($p_b = 0.0146$, $p_{ab} = 0.0001$), investigated at a higher rate ($p_b = 0.0013$, $p_{ab} < 0.0001$), and investigated for longer durations of time ($p_b = 0.0024$, $d_b = 0.80$, $p_{ab} = 0.0006$, $d_{ab} = 1.14$). In addition, we found that when compared to the physical scrape the physical scrape with puma urine was not investigated first more frequently, or investigated at a higher rate, but was investigated for longer durations of time ($p = 0.0465$, $d = 0.53$).

3.2. Communication behaviours

We recorded 762 visits by pumas of known age classes, including 37 632 s of puma activity, and a minimum of 25 individuals. Mature male pumas were

Table 3.

Differences in first detection and probabilities of detection between variables in the experimental treatments.

Variable pair	First investigation			Investigation rate			
	<i>N</i>	Percentage of first detection	<i>p</i>	df	Percentage investigated	<i>z</i> -score	<i>p</i>
0 vs a	33	0.61 vs 0.39	0.2962	118	0.40 vs 0.32	0.9519	0.3412
0 vs b	20	0.25 vs 0.75	0.0414	40	0.43 vs 0.91	-3.2733	0.0011
0 vs ab	21	0.14 vs 0.86	0.0015	40	0.38 vs 0.91	-3.5423	0.0004
a vs b	25	0.24 vs 0.76	0.0146	64	0.27 vs 0.67	-3.2063	0.0013
a vs ab	22	0.09 vs 0.91	0.0001	44	0.22 vs 0.96	-5.0906	<0.0001
b vs ab	28	0.50 vs 0.50	1.0000	58	0.70 vs 0.77	-0.5839	0.5593

The percentage of visits where a variable was investigated first is noted along with their *p*-values. Probability of detections between the variables are represented as percentages together with *z*-scores and *p*-values.

Table 4.

Differences in investigation duration between paired treatment variables in the experimental treatments.

Variable pair	df	Mean \pm SE	<i>p</i>
0 vs a	118	0.5 \pm 0.1 vs 0.8 \pm 0.2	0.2728
0 vs b	40	0.7 \pm 0.2 vs 4.8 \pm 1.0	0.0004
0 vs ab	40	0.5 \pm 0.2 vs 6.8 \pm 1.1	<0.0001
a vs b	64	0.4 \pm 0.1 vs 2.0 \pm 0.5	0.0024
a vs ab	44	0.9 \pm 0.5 vs 5.3 \pm 1.1	0.0006
b vs ab	58	1.9 \pm 0.4 vs 3.7 \pm 0.8	0.0465

The average duration of investigation in seconds and their standard error are noted, along with the pairwise *p*-values between the variables.

the most common visitor to community scrapes, with 73.1% of visits, in comparison to 22.1% for mature females and 3.4% for immature pumas, while 1.4% were visits by a mature male and female traveling together. Our analysis of the duration of visits to community scrapes did not find a significant difference among classes ($F_{2,522} = 1.59$, $p = 0.2040$), with an average visit duration of 57.6 s (95% CI = 52.2–63.1).

Our analyses of communication behaviours revealed significant differences among puma classes in the proportion of visits for each behaviour. Mature males exhibited scraping at 78.5% of visits, a significantly higher proportion of visits than the 13.6% for mature females ($\chi^2 = 202.67$, $df_{1,637}$, $p < 0.0001$, $\phi = 0.57$) and the 12.8% for immature pumas ($\chi^2 = 76.84$, $df_{1,529}$, $p < 0.0001$, $\phi = 0.39$) (Figure 2), while mature females and immature pumas did not differ significantly. Mature males exhibited olfactory investigation at 89.6% of visits, a significantly higher proportion than the 76.9% for immature pumas ($\chi^2 = 4.63$, $df_{1,529}$, $p = 0.0301$, $\phi = 0.11$). Mature females exhibited olfactory investigation at 85.7% of visits, and were not significantly different than mature males or immature pumas.

Mature males exhibited body rubbing at 12.4% of visits, a significantly higher proportion of visits than the 2.7% for mature females ($\chi^2 = 10.57$, $df_{1,637}$, $p = 0.0012$, $\phi = 0.14$) and the 0.0% for immature pumas ($df_{1,529}$, $p = 0.0153$, $\phi = 0.10$), while mature females and immature pumas did not differ significantly. Mature females exhibited flehmen responses at 30.6% of visits, a significantly higher proportion of visits than the 6.5% for mature males ($\chi^2 = 59.82$, $df_{1,637}$, $p < 0.0001$, $\phi = 0.31$) and the 7.7% for immature pumas ($\chi^2 = 7.30$, $df_{1,184}$, $p = 0.0069$, $\phi = 0.21$), while mature males

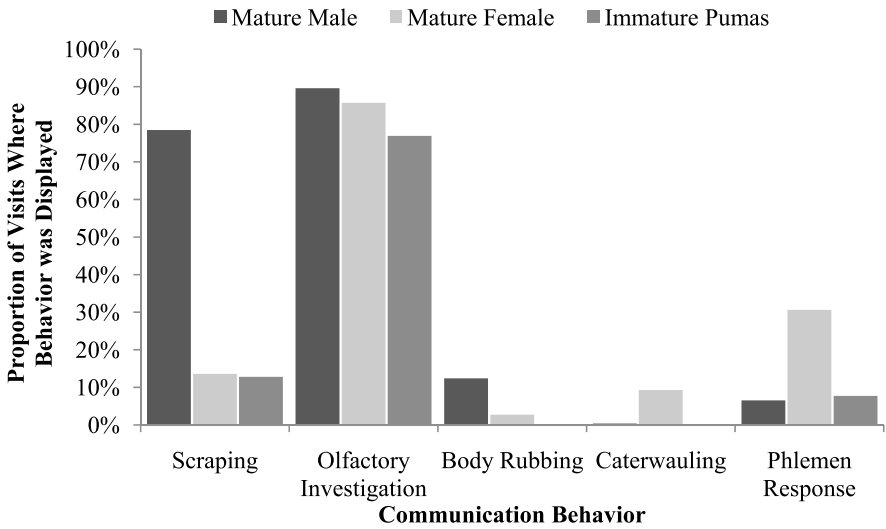


Figure 2. Proportion of visits where scraping and communication behaviours occurred for puma class. Behaviours include scraping, olfactory investigation, body rubbing, caterwauling and flehmen responses.

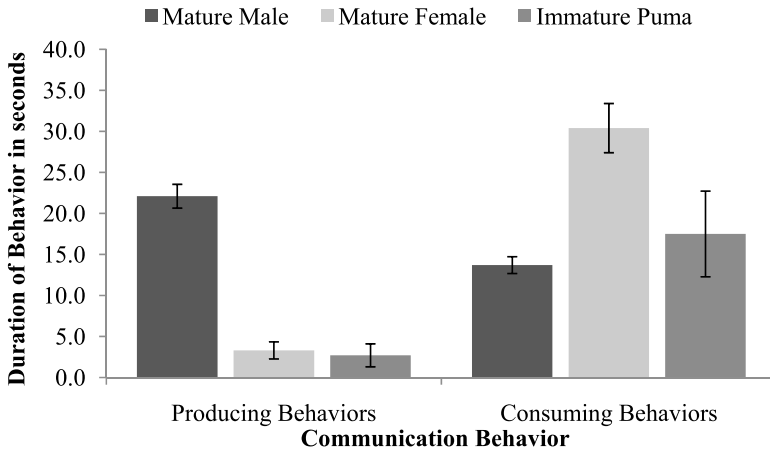


Figure 3. Mean duration in seconds of producing and consuming behaviours during visits to community scrapes by each class of pumas. The error bars represent the standard error. Producing behaviours include scraping, body rubbing and caterwauling, while consuming behaviours include investigating and flehmen responses.

and immature pumas did not differ significantly. Mature females exhibited caterwauling at 9.3% of visits, a significantly higher proportion of visits than the 0.4% for mature males ($df_{1,612}$, $p < 0.0001$, $\varphi = 0.24$) and the 0.0% for immature pumas ($df_{1,177}$, $p = 0.0401$, $\varphi = 0.39$), while mature males and immature pumas did not differ significantly.

The duration of producing behaviours was significantly different among puma classes ($F_{2,522} = 41.38$, $p < 0.0001$) (Figure 3). Our post hoc analysis revealed that mature males spent longer durations ($\bar{x} \pm SE = 22.1 \pm 1.5$ s) on producing behaviours than mature females ($\bar{x} \pm SE = 3.3 \pm 1.0$ s, $p < 0.0001$) or immature pumas ($\bar{x} \pm SE = 2.7 \pm 1.4$ s, $p < 0.0001$), but there was not a significant difference between immature pumas and mature females. The duration of consuming behaviours was significantly different among puma classes ($F_{2,522} = 14.31$, $p < 0.0001$). Our post hoc analysis revealed that mature females spent longer durations ($\bar{x} \pm SE = 30.4 \pm 3.0$ s) on consuming behaviours than mature males ($\bar{x} \pm SE = 13.7 \pm 1.0$ s, $p < 0.0001$) or immature pumas ($\bar{x} \pm SE = 17.5 \pm 5.2$ s, $p < 0.0001$), but there was not a significant difference between immature pumas and mature males.

4. Discussion

Our results suggest that pumas exhibit strong sexually dimorphic differences in their scrape communication behaviours, and pumas appear to be a good study species for further study of sexually dimorphic behaviours including mate selection. Male and female pumas exhibited differences in their duration of producing and consuming behaviours, as well as the proportion of communication behaviours used during visits. Our results support the hypothesis of Logan & Sweanor (2001, 2010) that the differences in use of communication behaviours at community scrapes can be explained through different life history patterns and evolutionary reproductive strategies of the sexes. Male strategy appears to be based on regular visitation and the production of signals for potential mates to find. In contrast, female visitation is infrequent, in order to limit potentially dangerous encounters with males which could lead to infanticide. Female strategy is apparently to limit risk, and then visit community scrapes for short time periods just before and during oestrus, and use these visits to assess potential mates.

We found that mature males spent longer durations exhibiting producing behaviours than mature females, and also exhibited scraping and body rub-

bing behaviours at a higher proportion of visits than mature females. Mature males have large home ranges, and need to leave sign for potential mates to find as well as for territorial defence. Dominance has been linked to frequency of scent-marking in mice (Hurst & Benyon, 2004; Thonhauser et al., 2013), and male strategy may be based on trying to produce as many signals as possible for potential mates to find. The bi-functional role of scraping for territorial maintenance and advertisement for mates suggests male strategy is based on production of signals for others to find. However, although scraping behaviour was frequently used during visits by mature males, there appeared to be variation in both the duration of visits and the number of scrapes created. We hypothesize that when males detect recent visits by female pumas they increase the duration of their visits and the number of scrapes they create. Similar to Logan & Sweanor (2001), we never recorded pumas spraying urine, while in contrast to Harmsen (2010), we never recorded pumas scraping with their front feet, and we are doubtful that pumas exhibit these behaviours in our study area. We found body rubbing behaviour to be used at a higher proportion of visits by mature males, and while we are unclear what triggers body rubbing behaviours in pumas, we hypothesise that it is used as an additional form of communication attempts for potential mates.

Mature females were less frequent visitors to community scrapes, and spent less time using producing behaviours. Although there are more mature females than mature males in any given puma population (Sunquist & Sunquist, 2002), mature females were less frequent visitors, accounting for 22.1% of visits. The simplest explanation is that mature females visit for short bouts of temporally clustered visits while in oestrus, as hypothesized by Logan & Sweanor (2001, 2010). However, females may not just appear when ready to mate, and their visits to community scrapes may instead occur in a progression, from investigation and assessment to advertising their receptive status, and eventually to mating. Logan & Sweanor (2001) rarely documented scraping behaviour in females, and believed that females squatted and urinated on scrapes made by males more frequently than making scrapes themselves. Through the use of video cameras we also documented female pumas both scraping and urinating on top of scrapes made by male pumas, but found that among females scraping was actually more common than urinating on the scrapes of males (13.6% to 2.2%, respectively). We found that caterwauling behaviour was more frequently used by mature females, only being used by mature males at 0.4% of visits. Caterwauling in

some instances is likely more effective than scraping to advertise for potential mates, for instance, caterwauling can be used for immediate attraction and to advertise from a distance (Logan & Sweanor, 2001).

We found that mature females spent longer durations exhibiting consuming behaviours than mature males, while also exhibiting flehmen response behaviour at a higher proportion of visits. Mellen (1993) found that the use of the flehmen response behaviour by felid species was common at each investigation of urine; however we found flehmen response behaviour to be less frequently used by wild pumas (it occurred at 11.8% of visits). Rather than being a difference between pumas and other felid species, Mellen's (1993) findings may have been a by-product of studying felids in captivity, where the usually solitary felids come in contact with scent-markings more often than in the wild. For example, de Boer (1977) found that urine less than 4 h old triggered a flehmen response significantly more often than urine which was over 24 h old. Mellen (1993) also found that flehmen response behaviour was more common in male felids, which contradicted our findings with wild pumas. We hypothesize that the longer durations of consuming behaviours and the higher rate of flehmen response behaviour by females is due to females using visits to assess potential mates. In contrast, male pumas apparently spend shorter durations investigating competitors, and instead may only use flehmen response behaviour to investigate scent left by females or unknown individuals, both of whom are less frequent visitors to community scrapes.

The scraping and associated communication behaviours appear to develop with age, and to only be used by mature females when traveling without cubs. Intraspecific strife is a frequent source of mortality in juvenile pumas, with mature males killing cubs and sub-adult males (Logan & Sweanor, 2001, 2010). Logan & Sweanor (2001) also documented that over 25% of encounters between mature males and females which were not in oestrus were violent. For this reason, it increases survival and hence fitness for both immature pumas and females with cubs to not openly advertise their presence at community scrapes. We were unable to find a significant difference between females with and without cubs, possibly due to our low sample size of females with cubs visiting community scrapes, however females may use community scrapes differently based on whether they are with or without cubs. For example, females with cubs were never recorded displaying either scraping or caterwauling behaviours, and we hypothesise that females with

cubs are more closely aligned to immature pumas in regards to being 'non-participants' in behaviours at community scrapes.

Our experimental treatments showed that the physical scrape and urine components had different roles, and were both necessary to scrape communications. Experimental components with a physical scrape were detected first more often and at a higher proportion of visits than urine alone, while urine alone was not significantly different than the control. Additionally, pumas did not show difference in first investigation or proportion of investigation for just physical scrape in comparison to physical scrape with puma urine. However, there was a significant difference between the two variables in regards to duration of investigation with the physical scrape with urine being investigated for a significantly longer duration than just the physical scrape. These results show that pumas rely on the physical scrape to locate communication attempts by other pumas, and then use the urine to convey and interpret the communication itself.

Scrapes are the most obvious signals pumas leave on the landscape, and males appear to use scrapes to compete against each other. The scrapes created appear to compete against each other, as the more stimuli available the less experimental treatments were detected and investigated. For example, the proportion of visits where urine was investigated steadily decreased in response to stimuli, from 32% against control to 27% against a physical scrape and 22% against a physical scrape with urine; and the duration of investigation of physical scrapes with urine decreased from 6.7 s against control to 5.3 s against urine and 3.7 s against the physical scrape. Some male pumas may use this to their advantage to create dishonest signals in order to increase their attractiveness to females. For example, some individual males may create an excess of scrapes in order to overwhelm females with stimuli and increase the probability that their scrapes are detected over that of competitors. Pumas intentionally leave scrapes as signals for other pumas, however scrapes are made in areas frequented by other species, and they may also be using scrape communications as cues. For example, numerous scavengers have been noted at puma kills (Ruth & Murphy, 2010), and it is possible that the mammalian scavengers are using puma scent communications to find and track the pumas to their kills.

The importance of the visual component of physical scrapes reinforces the importance of community scrapes, and could be applied to puma census efforts. Each individual scrape is an attempt at communication, and if pumas created scrapes in random areas they would be much more difficult for the

signals to be received by other pumas. This is especially true in species with spatially dispersed populations, such as pumas or other solitary carnivores, where having regular areas for communication (i.e., community scrapes) increases their likelihood of being found. Puma populations have historically been difficult to census, and many wildlife professionals believe the only truly accurate way to census puma populations is through long-term study of the population with known individuals through radio-telemetry or GPS collars (Cougar Management Working Group, 2005). However, many attempts are still made to develop accurate census techniques for puma populations (Cougar Management Working Group, 2005; Choate et al., 2006), and using census techniques involving camera traps (see Kelly et al., 2008) at community scrapes rather than random areas would likely increase the rate of capture and hence success. In addition, there are numerous efforts, either for population census or study capture, to detect pumas through various types of scent lures often without great success (Long et al., 2003; Choate et al., 2006; Walker & Novaro, 2010). However, the findings of this study show that the use of scent lures is not the best strategy for pumas and possibly other felids, and instead, the use of visual lures (possibly in conjunction with auditory lures) would be more effective.

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