



## Original Investigation

Communal latrines act as potentially important communication centers in ocelots *Leopardus pardalis*Torrey W. Rodgers<sup>a,b,\*</sup>, Jacalyn Giacalone<sup>b,c</sup>, Edward J. Heske<sup>a,d</sup>, Natalie C. Pawlikowski<sup>e</sup>, Robert L. Schooley<sup>f</sup><sup>a</sup> Department of Animal Biology, University of Illinois, 505 S. Goodwin Avenue, Urbana, IL 61801, USA<sup>b</sup> Smithsonian Tropical Research Institute, 0843-03092 Balboa, Ancon, Panama<sup>c</sup> Montclair State University, 1 Normal Avenue, Montclair, NJ 07043, USA<sup>d</sup> Illinois Natural History Survey, Prairie Research Institute, University of Illinois, 1816 S Oak Street, Champaign, IL 61820, USA<sup>e</sup> School of Integrative Biology, University of Illinois, 505 S. Goodwin Avenue, Urbana, IL 61801, USA<sup>f</sup> Department of Natural Resources and Environmental Sciences, University of Illinois, 1102 S. Goodwin Avenue, Urbana, IL 61801, USA

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## ABSTRACT

In solitary carnivores, scent marking is an important form of communication among individuals. We examined the extent of potential communication among ocelots (*Leopardus pardalis*) at communal latrine sites at the population level. We used a combination of camera-trapping and noninvasive genetics to monitor 18 ocelot latrines in an isolated population on Barro Colorado Island in the Republic of Panama. We found that 72% of monitored ocelot latrines were used by multiple individuals of both sexes, with a mean of 3.0 individuals (range 1–9) per year using each latrine. One highly used latrine was visited by 17 different individuals including 11 males and 6 females over the course of 6 years. Based on visits to the same latrine within 10 days of one another, potential for scent communication among individuals was high. Males had the potential to communicate with a mean of 5.9 other individuals (range 2–14), and females had the potential to communicate with a mean of 4.5 other individuals (range 3–12) at latrines. We conclude that communal latrines are important centers of scent communication for *Leopardus pardalis*.

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## Introduction

In carnivore species that live at low density, direct communication between individuals through visual or acoustic signals is infrequent. In these species scent marking, in which an olfactory chemical signal persists long after the signaler has departed, is responsible for a large share of communication among individuals (Darden et al., 2008; Gorman and Trowbridge, 1989). Scent marking using urine or feces is common in carnivore species (Macdonald, 1980) and can function in territorial spacing between individuals (Richardson, 1993), maintaining dominance hierarchies (Clapham et al., 2012) and communicating breeding condition between members of the opposite sex (Molteno et al., 1998; Rishi, 2012; Vogt

et al., 2014). In the family Felidae, scent marking is widespread (Mellen, 1993; Rishi, 2012; Vogt et al., 2014), and in some species established latrine sites are repeatedly used for the deposition of urine and feces (Bailey, 1974; Manfredi et al., 2006; Marnewick et al., 2006; Soler et al., 2009). These latrine sites may play a central role in communication networks and transfer of information.

Ocelots (*Leopardus pardalis*), a medium-sized Neotropical felid, use latrines for scent marking, and multiple individuals of both sexes often use the same latrine site (Moreno and Giacalone, 2014; Rodgers et al., 2014, 2015). We conducted a study to examine the extent of shared latrine use by ocelots and the potential for information exchange among individuals at latrines. We used a combination of camera trapping and noninvasive genetics to monitor 18 ocelot latrines. Although other studies have documented latrine use in felid species (Bailey, 1974; Manfredi et al., 2006; Marnewick et al., 2006; Napolitano et al., 2008; Soler et al., 2009) our study goes further by examining the extent of their use by multiple individuals of both sexes and thus their potential importance in communication networks.

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## Material and methods

### Study area

Field work was conducted on Barro Colorado Island (BCI), a 1.54 km<sup>2</sup> island in the Panama Canal waterway, at a research station operated by the Smithsonian Tropical Research Institute (Fig. 1). BCI (9° 10' N, 79° 51' W) sits within Gatun Lake, an artificial body of water created in 1912 by the damming of the Chagres River to create the Panama Canal, and is part of the protected 54-km<sup>2</sup> Barro Colorado Nature Monument. Vegetation is tropical moist forest, and topography is dominated by hills that reach a maximum elevation of 165 m above sea level. Mean temperature is 27 °C with an average annual precipitation of 2600 mm, with 90% of rainfall occurring from May through November (Leigh, 1999). Other carnivore species on the island include tayra (*Eira barbara*), white-nosed coati (*Nasua narica*), and crab-eating raccoon (*Procyon cancrivorus*). Pumas (*Puma concolor*) and jaguars (*Panthera onca*) are not resident, but they do infrequently visit the island for short periods.

### Study species

Ocelots are a medium sized felid with a wide geographic range stretching from northern Argentina to the southern United States (Nowell and Jackson, 1996). Although their overall conservation status is least concern (IUCN Red List of Threatened Species 2014.3), many populations are threatened or endangered due to habitat loss, particularly in the northern portion of their range (Janečka et al., 2011). Ocelot population density and home range size varies considerably between populations based on environmental factors (Di Bitetti et al., 2008; Moreno et al., 2012); however, on BCI density is extremely high (Rodgers et al., 2014) and home ranges are relatively small (1.5 km<sup>2</sup> for females and 3.5 km<sup>2</sup> for males – Moreno et al., 2012). Ocelots do not have a distinct breeding season, rather they breed year round, with reproductive females siring litters of 1–2 kittens approximately every 2 years (Nowell and Jackson, 1996).

### Latrine surveys

Our objective during surveys was to locate as many ocelot latrines as possible. The locations of five active latrines were already known prior to our search period. To find additional latrines, we walked >510 km of transects on and off trail throughout the island.

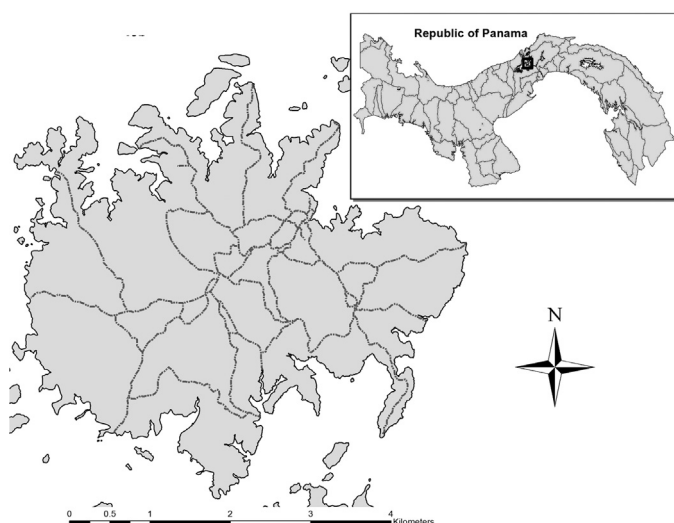


Fig. 1. Map of Barro Colorado Island in the republic of Panama, study site for research on communal latrine use in ocelots (*Leopardus pardalis*). Dashed lines indicate trails.

Once a latrine was located, all scats were collected for noninvasive genetic analysis. Thirteen additional latrines were found by our searches, resulting in a total of 18 latrines. Trail cameras (Reconyx RC55, Reconyx Inc., Holmen, Wisconsin) were placed at 16 of these. All latrines were then revisited every 4–7 days to check cameras and to collect additional scats. Removing scats for noninvasive genetics could have had some effect on future scent-marking behavior, however, animals continued to return and mark latrines after scats were removed. Latrine searches, scat collection, and most camera trapping were conducted over a 99-day period from 29-January to 6-May 2012. In addition, four camera traps were left on latrines for longer periods, one for 81 days in 2008–2011, one for 344 days in 2012–2014, one for 554 days in 2012–2014, and one for 861 days in 2008–2014.

### Noninvasive genetics

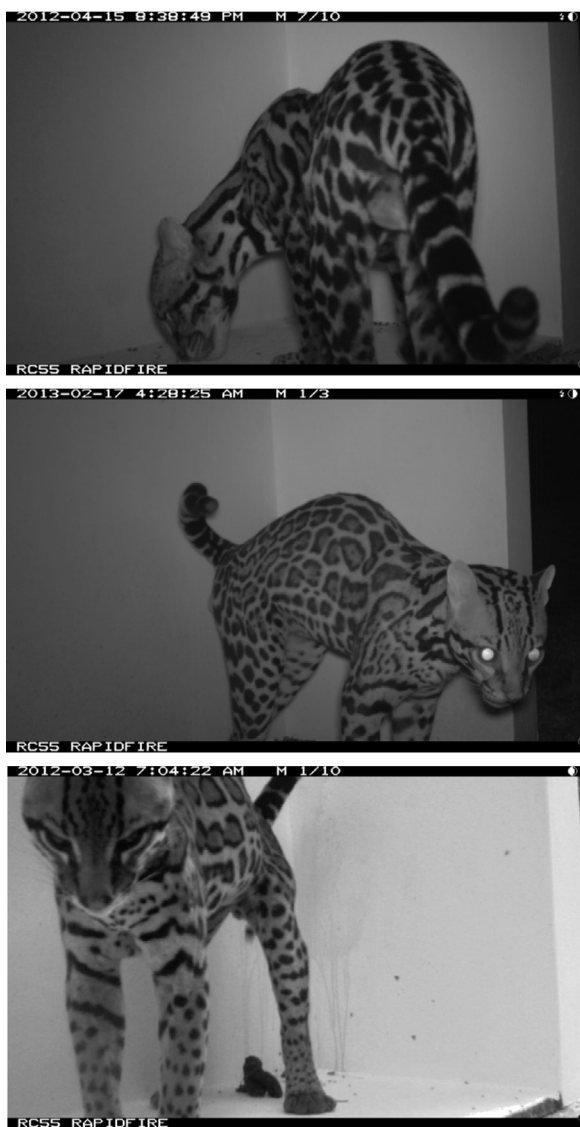
DNA was extracted from scats using the Qiagen QIAamp DNA stool mini kit (Qiagen, Valencia, California) following the manufacturer's recommendations. For species identification, we amplified a 126-bp fragment of the mitochondrial gene ATP6 by polymerase chain reaction (PCR) using primers ATP6-DF3 and ATP6-DR1 following conditions from Chaves et al. (2012). PCR products were sequenced on an Applied Biosystems 3730xl DNA analyzer, and resulting sequences were compared to reference sequences using the online tool DNA Surveillance Carnivora (Chaves et al., 2012).

To identify individuals, scat samples were genotyped at 4 microsatellite loci (FCA075, FCA077, FCA088, and FCA132) originally developed for the domestic cat (*Felis catus*) (Menotti-Raymond et al., 1999). We initially screened 22 loci previously found to be variable in ocelots (Janečka et al., 2011). The 4 loci used for individual identification were selected based on degree of variability, success of amplification, and ease and clarity of allele scoring (Rodgers et al., 2015). As DNA from noninvasively collected fecal samples is often low quality and prone to genotyping errors such as allelic dropout and false alleles (Broquet et al., 2007; Taberlet et al., 1999), we used a multiple tubes approach (Taberlet and Fumagalli, 1996) whereby each sample was genotyped 3–9 times until reliable consensus genotypes were obtained. Genotypes were only accepted as reliable if a minimum of 3 identical heterozygote profiles, or 5 identical homozygote profiles, were observed (for PCR conditions see Rodgers et al., 2014). Checks for departure from Hardy-Weinberg equilibrium, and probability of individual identity (Waits et al., 2001) were calculated using the program GENEALX (Peakall and Smouse, 2006).

For sex identification, we used felid-specific primers that amplify a 200-bp segment of the AMELY gene (Murphy et al., 1999), which is only present on the Y-chromosome of males (for PCR conditions see Rodgers et al., 2014). PCR amplifications were performed in triplicate along with male and female positive controls and a negative control, and PCR products were visualized on agarose gel. Samples were identified as male if they showed amplification of the Y-linked marker for all 3 replicates, and were identified as female if no amplification was observed (Rodgers et al., 2015).

### Camera trapping

Unique spot patterns were used to identify individual ocelots from camera-trap photos taken at latrines (Trolle and Kery, 2003). Sex was determined from photographs based on presence or absence of conspicuous testicles that are highly visible in males. These data were used along with our noninvasive genetic data to determine the minimum number of individuals of each sex using each latrine. Potential for communication between individuals was defined as visits to the same latrine within 10 days of one another. The period of 10 days was chosen as a reasonable time for



**Fig. 2.** Three ocelot (*Leopardus pardalis*) behaviors observed at communal latrine sites by camera traps on Barro Colorado Island in Panama. From top to bottom: sniffing, spraying, and defecating.

persistence of a deposited chemical scent. This is a conservative time frame as the strong urine scent at ocelot latrines is perceptible by the human nose for weeks after a latrine has been used, as has been documented in other studies (Vogt et al., 2014). Photo sequences were also used to categorize the behaviors ocelots engaged in during each latrine visit. Behavior categories were sniffing, urine spraying, or defecating (Fig. 2). These behaviors were hierarchical; animals that sprayed nearly always sniffed, and animals that defecated nearly always sniffed and sprayed.

## Results

### Noninvasive genetics

Sixty-three scats were collected from 18 ocelot latrines on BCI, and 55 (87%) were genetically confirmed as being from ocelots (with the other 13% failing to amplify with PCR). From these 55 scats, we obtained complete 4-locus genotypes from 43 samples (78%), which consisted of 12 unique genotypes and 31 recaptures

**Table 1**

Mean number of individual ocelots (*Leopardus pardalis*) detected per latrine per year with noninvasive genetics (NG), camera trapping (CT), or both (NG + CT), on Barro Colorado Island, Panama. Communal latrines are latrines where >1 individual was detected. Values in parentheses are ranges.

	Males	Females	Total
Noninvasive genetics (NG)	0.88 (0–3)	0.75 (0–2)	1.63 (1–5)
Camera trapping (CT)	1.63 (0–5)	1.22 (0–5)	2.85 (1–9)
NG + CT All latrines	1.70 (0–5)	1.30 (0–5)	3.00 (1–9)
NG + CT Communal latrines	1.95 (1–5)	1.50 (0–5)	3.45 (2–9)

from 16 latrines. Six individuals were identified as male, and six as female. All 4 loci were in Hardy–Weinberg equilibrium and the number of alleles per locus was 3–6. Based on allele frequencies within the sampled population, probabilities of individual identity among unrelated individuals  $P_{(ID)}$  was 0.00031, and among siblings  $P_{(ID)sibs}$  was 0.038 (Waits et al., 2001). Mean number of individuals recorded per latrine per year from noninvasive genetic sampling was 1.63 (range 1–5; Table 1).

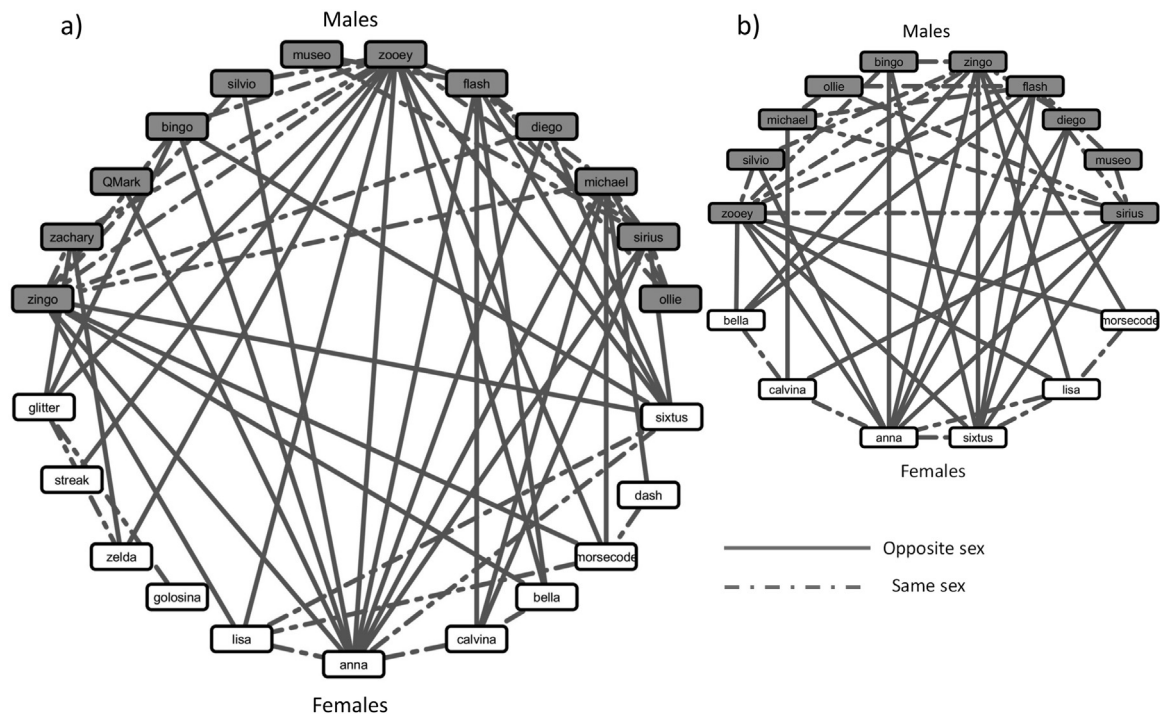
### Camera trapping

We observed 353 ocelot visits at 16 latrines by 25 individual ocelots (14 males and 11 females). More visits were by males (62%), than by females (38%). Sniffing was observed in all visits, spraying in 65% of visits, and defecation in 22% of visits. The frequency of behaviors differed between males and females ( $X^2 = 7.25$ ,  $p = 0.027$ ); males sprayed more frequently than did females (73% vs. 52% of visits) whereas females defecated more frequently than did males (27% vs. 19% of visits). Mean number of individuals recorded per latrine per year from camera trapping was 2.85 (range 1–9; Table 1). At 14 of the 16 latrines where both camera trapping and noninvasive genetics were used, camera trapping identified a greater number of individuals. Camera trapping also detected significantly more individuals per latrine on average than did noninvasive genetics (Mann–Whitney,  $Z = 2.47$ ,  $p = 0.0135$ ). This is not surprising as noninvasive genetics only recorded individuals who defecated at latrines while camera trapping also included individuals who visited latrines to sniff or spray.

Of the 18 total latrines monitored by noninvasive genetics, camera trapping, or both, 13 (72%) were visited by >1 individual and the remaining 5 (18%) were visited by only 1 individual during our monitoring period. Mean number of individuals recorded per latrine per year from both methods combined was 3.0 (range 1–9; Table 1). Of those latrines visited by multiple individuals, the mean number of individuals recorded per latrine per year was 3.45 (range 2–9). This shared use included a mean of 1.95 males per latrine per year (range 1–5), and mean of 1.5 females per latrine per year (range 0–5). Because most latrines were only monitored for a portion of the year (>4 months), the true number of individuals per latrine per year is likely higher. At the one latrine that was monitored off and on for nearly 6 years, a total of 17 individuals were recorded including 11 males and 6 females.

The potential for olfactory communication among individuals at latrines was high based on visits to the same latrine within 10 days of one another (Fig. 3). Males had the potential to communicate with a mean of 5.9 other individuals (range 2–14). Of these, a mean of 2.6 were females (range 1–6), and a mean of 3.3 were other males (range 1–8). Females had the potential to communicate with a mean of 4.5 other individuals (range 3–12). Of these, a mean of 2.9 were males (range 1–9), and a mean of 1.6 were other females (range 1–3).





**Fig. 3.** Potential for olfactory communication among individual ocelots (*Leopardus pardalis*) at communal latrine sites on Barro Colorado Island, Panama based on visits to the same latrine within 10 days of one another. (a) Communication network based on all monitored latrines, and (b) network from a single, heavily used latrine.

## Discussion

Our results clearly demonstrate that there is great potential for olfactory chemical communication among individual ocelots at communal latrines. Communal latrines were used frequently by members of both sexes to gather information by sniffing, and to deposit information by spraying and defecating. Finding latrines in dense tropical forest is difficult, so there were certainly many latrines within our study area that we did not locate, and thus were not accounted for in our communication networks. Hence, potential for communication at latrines is certainly even greater than identified by this study, and is clearly an important form of communication between individuals of *Leopardus pardalis*.

There are three general functions of scent marking in solitary carnivores, and these are not mutually exclusive (Muller and Manser, 2008). Scent marking can be used to (1) demarcate territorial boundaries and maintain spacing between individuals of the same sex (Richardson, 1993), (2) communicate dominance (Clapham et al., 2012), and (3) advertise breeding condition to members of the opposite sex (Molteno et al., 1998; Rishi, 2012; Vogt et al., 2014). In addition, wildcats (*Felis silvestris*) may use feces to mark favorable hunting areas (Piñeiro and Barja, 2015). Unfortunately, we do not have detailed enough data to determine with certainty which of these functions is being served by communal latrine use in ocelots. We do have considerable long-term insight regarding the social and spatial organization of this particular population (Rodgers et al., 2014, 2015), however, which enables us to propose potential functions of scent marking among male and female ocelots on Barro Colorado Island.

Maintenance of territorial boundaries seems an unlikely function of communal ocelot latrines, because latrines were marked by many individuals, as opposed to one or two individuals repeatedly marking his or her territorial boundary at a latrine. Females visiting latrines were sometimes in estrus based on camera trap photos, so the function of advertising breeding condition to potential mates seems likely. Another possibility is that females use latrines for individual recognition of favored or long term mating partners (Palagi

and Dapporto, 2006; Thom and Hurst, 2004). Two individual ocelots were never observed at a latrine at the same time, however, so latrines appear to serve only as message boards, and not meeting places for mating or other social activities. For males, signaling to females that they are in the area and available to breed is one possible function of latrine marking, or males may be using latrines to communicate dominance to other males to minimize direct violent confrontation. The latter seems especially plausible in the BCI population, because population density is extremely high (Rodgers et al., 2014), and male-male spatial overlap is greater than expected by chance (Rodgers et al., 2015). Thus mechanisms to avoid violent confrontations, while still advertising dominance, should be particularly important.

The locations of ocelot latrines were clearly chosen to optimize the persistence of scent in the wet Neotropical environment. Nonrandom placement of scent marks, and selection of substrate conducive to scent communication has been observed in other felid species as well (Piñeiro and Barja, 2015; Robinson and Delibes, 1988; Soler et al., 2009). Ocelot latrines were typically located in conspicuous, protected locations such as in cavities or overhanging buttresses of large trees, underneath buttresses of fallen trees, or underneath human structures. Most latrine locations were protected from above, and thus served to shelter deposited feces and urine from rain and sun. This placement would keep urine or feces from being washed away, and would thus allow chemical scents to persist far longer than if they were deposited in open areas. Bare or hard surfaces were also generally chosen for deposition of scent as opposed to areas of the forest floor covered in leaf litter. Termites, ants, and microbes seem to find scats more easily when they are in contact with soil and leaves, and they can consume most of a scat in a few days.

Scent marking at communal latrines has been documented in several felid species including bobcats (*Lynx rufus*; Bailey, 1974), and cheetahs (*Acinonyx jubatus*; Marnewick et al., 2006), however this behavior seems to be especially common among species within the genus *Leopardus*. In addition to ocelots, communal latrine use has been documented in Geoffrey's cat (*Leopardus geoffroyi*;

Johnson and Franklin, 1991; Manfredi et al., 2006; Soler et al., 2009), Andean cat (*Leopardus jacobita*; Napolitano et al., 2008) and pampas cat (*Leopardus colocolo*; Napolitano et al., 2008). Thus, species from this genus may be good candidates for further research into the function of scent marking in felids.

Although it has long been known that scent marking with urine and feces plays an important role in carnivore communication, few studies have examined scent communication networks at the population level. Advances in camera trapping technology and integration with methods such as noninvasive genetic identification of individuals and sex from feces (Rodgers and Janečka, 2013) provide improved approaches for such research in carnivores, especially for species that repeatedly use communal latrines. The logical next step is to design studies to test hypotheses regarding the type of information being shared through scent communication, and the resulting functions. Such empirical tests in solitary carnivores are rare. Our study sets the stage for such research by demonstrating that the potential for information sharing among individuals of both sexes through scent marking is high. Communal latrine sites clearly act as important centers for scent communication networks in *Leopardus pardalis* and this is also likely true for other solitary carnivores.

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