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VIDEO ARTICLE

The scent of your enemy is my friend? The acquisition of large carnivore scent by a smaller carnivore

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Abstract Scent marking is critical to intraspecific communication in many mammal species, but little is known regarding its role in communication among different species. We used 4 years of motion-triggered video to document the use of scent marking areas—termed "community scrapes"—by pumas (*Puma concolor*) (http://www.momo-p.com/showdetail-e.php?movieid=momo160812pc01a) and other carnivore species. We found that gray foxes (*Urocyon cinereoargenteus*) routinely rubbed their cheeks on puma scrapes (http://www.momo-p.com/showdetail-e.php?movieid=momo160812uc01a), and tested a series of hypotheses to determine its function. We found that gray foxes selected puma scrapes over other objects, and cheek rubbing by foxes was also correlated with how recently a puma had visited the scrape, suggesting that foxes were intent upon accumulating fresh puma scent. Cheek rubbing by foxes was not correlated with their breeding season or with how recently another fox had visited the site. Finally we found a cascading pattern in the occurrence of pumas, coyotes (*Canis latrans*) and gray foxes at community scrapes, suggesting that gray foxes may use puma scent to deter predation. This is the first published study to find evidence of a subordinate species using the scent of a dominant species to communicate with heterospecifics. The behavioral cascade we found in scent marking patterns also suggests that scent marking could be a mechanism that impacts the distribution and abundance of species. Additional videos pertaining to this article include http://www.momo-p.com/showdetail-e.php?movieid=momo160812uc02a, and http://www.momo-p.com/showdetail-e.php?movieid=momo160812uc03a.

Keywords Cheek rubbing · Communication · Interspecific interactions · *Puma concolor* · Scent marking · *Urocyon cinereoargenteus*

Introduction

Scent marking is an integral aspect of communication for many mammals (Ralls 1971; Johnson 1973). Scent marking is used to deposit volatile chemical compounds to communicate signals (Ralls 1971; Johnson 1973), and is often used as an indirect method of communicating with conspecifics (Roper et al. 1993; Bel et al. 1999; King and Gurnell 2007; Allen et al. 2015a). Scent marking is an important aspect of intraspecific communication for mate selection (Bel et al. 1999; Allen et al. 2015a) and advertising the use of a territory (Roper et al. 1993; King and Gurnell 2007), as well as for other functions such as noting food resources (Henry 1977; Pineiro and Barja 2015).

Although there are many studies on intraspecific communication, there is a general lack of current literature on how scent marking is used for interspecific communication (but see Rostain et al. 2004; Apfelbach et al. 2005). There is some literature exploring how animals respond to vocalizations of heterospecifics (Shriner 1998; Magrath et al. 2015), and the lack of studies on interspecific communication through scent marking may be due to its complexity and difficulty in studying. Based on the lack of literature about interspecific scent marking it would be

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reasonable to conclude that interspecific communication through scent marking does not frequently occur. It is more likely, however, that scent marking is an important aspect of interspecific interactions in mammal communities of which we remain remarkably unaware. Mammals within given communities are known to partition resources (Schoener 1974), and subordinate species avoid dominant ones both spatially and temporally (Ordiz et al. 2012; Darnell et al. 2014; Wang et al. 2015). Scent marking may be key to both partitioning resources and avoidance tactics, and it is therefore important to document instances of interspecific communication and scent marking to understand their functional and adaptive significance.

Over the course of 4 years, we documented gray foxes (*Urocyon cinereoargenteus*) visiting scent marking areas termed "community scrapes" (Allen et al. 2014). Community scrapes are scent marking areas used by the carnivore guild (Allen et al. 2015a), including pumas (*Puma concolor*), who use the area for territorial marking and mate selection (Allen et al. 2014, 2015a, 2016). Community scrapes are defined as the broader areas across which scent marking occurs, as opposed to the "individual scrape" created by an individual puma during a scent marking event (Allen et al. 2014) (Fig. 1, http://www.momo-p.com/showdetail-e.php?movieid=momo160812pc01a). The gray foxes we observed frequently used olfactory investigation and then left urine scent marks at these areas. Less frequently gray foxes exhibited cheek rubbing behavior, where they rubbed their cheek, jaw, and neck on puma individual scrapes or other nearby objects (Fig. 2, http://www.momo-p.com/showdetail-e.php?movieid=momo160812uc01a). The use of puma community scrapes for scent marking, and particularly the cheek rubbing behavior, by gray foxes suggests some aspect of interspecific scent marking was occurring. We could not find any reference in the literature to interspecific communication through cheek rubbing; thus we examined gray fox behavior of cheek rubbing on puma individual scrapes further to evaluate its functional significance through testing a series of hypotheses.

Fig. 1 A video of a puma creating an individual scrape. The area in view of the video is a community scrape

Fig. 2 A video of a *gray* fox exhibiting cheek rubbing behavior on an individual scrape made by a puma

Cheek rubbing, where an animal rubs its cheek, chin, neck, or shoulder on objects, is a form of scent marking that is infrequently documented compared to marking with urine or feces, but is nevertheless exhibited by many mammals (Reiger 1979; Mellen 1993; Gosling and McKay 1990; Bel et al. 1999; Allen et al. 2014). Some species, like marmots (*Marmota marmota*) primarily scent mark through cheek rubbing (Bel et al. 1999), and dominant rabbits (*Oryctolagus cuniculus*) were found to exhibit cheek rubbing more frequently than subordinate individuals (Mykytowycz 1965). These observations suggest that dominance can be exhibited through cheek rubbing as well as through other forms of scent marking. These species are easily observed, and the infrequency of documentation of cheek rubbing for many species could be due to the difficulty of observation; cheek rubbing could be of greater importance than generally recognized. Cheek rubbing releases compounds from the sebaceous gland, allowing the animal to deposit its scent on an object (Ralls 1971; Johnson 1973). At the same time, cheek rubbing provides the opportunity for an animal to accumulate scent from the environment onto itself (Johnson 1973; Gosling and McKay 1990).

We first determined baseline behavior for gray foxes at puma community scrapes and how this varied when they exhibited cheek rubbing. This included documenting their frequency of display of olfactory investigation and urine scent marking, and the duration of a visit during which they exhibited cheek rubbing behavior in contrast to times they did not. Next we generated two alternative hypotheses to evaluate the role interspecific communication played in this behavior; during cheek rubbing: (1) gray foxes may be depositing their own scent onto the substrate in order to compete with other conspecific individuals or advertise for mates; alternatively (2) gray foxes may be transferring

puma scent onto themselves either for mate attraction or predator avoidance.

Canids and other carnivores are well known for rubbing themselves on various scents (Johnson 1973; Gosling and McKay 1990). If cheek rubbing behavior by gray foxes on puma individual scrapes is for mate attraction, we expected a significant peak in the display of this behavior in late winter to spring to coincide with the peak of the breeding season. Alternatively, gray foxes may rub puma scent onto themselves in order to dissuade predation by larger predators, including coyotes (*Canis latrans*) and bobcats (*Lynx rufus*). Smaller carnivores have been shown to increase caution and alter their feeding behavior when exposed to the scent of larger carnivores (Garvey et al. 2016). If coyotes and bobcats exhibit caution when exposed to puma scent, gray foxes may be able to deter intraguild predation by applying puma scent to themselves and potentially causing a coyote or bob cat to hesitate in an attack and allow the gray fox to escape.

We tested the following predictions: if gray foxes are depositing scent, they should be cheek rubbing on other available objects as much as on puma individual scrapes. In addition, because scent is ephemeral, if gray foxes were depositing scent to communicate to conspecifics, we expected the exhibition of cheek rubbing behavior to have a significant positive relationship with how recently a gray fox had visited, because they were likely responding to the most recent visit of a conspecific. Alternatively, if gray foxes aimed to acquire puma scent, we predicted that greater than 50 % of the objects on which they cheek rubbed should be puma individual scrapes. We further expected that gray fox cheek rubbing would have a significant positive relationship with how recently a puma created the individual scrape, because they would be trying to accumulate the puma scent before it dissipated. Testing whether cheek rubbing behavior is for predation avoidance is more difficult, as we could not directly test the success of such a strategy. Therefore, we instead tested for differences in the relative abundance of the four carnivore species (gray fox, bobcat, coyote, puma) at community scrapes, in order to assess whether or not puma scent dissuaded bobcats and coyotes from using these areas, and whether our predation avoidance hypothesis was worth follow-up study in the future.

Materials and methods

Study area

We conducted our study in a 1700 km^2 area in the Santa Cruz Mountains, including parts of Santa Cruz, San Mateo, and Santa Clara Counties of California. Detailed descriptions of the study area are available from Wilmers et al. (2013) and Allen et al. (2014). 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. An arterial highway (Highway 17) bisected the study area. Major habitat types in the study area varied with distance from the coast, and included coastal scrub, annual grassland, redwood (*Sequoia sempervirens*) forest, and chaparral. Elevation ranged from sea level to 1155 m. The climate is best described as mild Mediterranean, with the majority of rainfall occurring from November to April.

Compliance with ethical standards

The data collected in this manuscript were obtained through non-invasive methods, and no animals were handled, drugged, or harmed during the course of the study. All protocols were performed within the guidelines set by the University of California and the American Society of Mammalogists. The authors have no known conflicts of interest.

Field methods

We documented 299 puma community scrapes from 2008 to 2015 using a custom algorithm to find potential community scrapes followed by field visits to confirm or deny (Allen et al. 2014). We then set up motion-triggered video cameras with infrared flash (Bushnell Trophy Cam, Overland Park, KS) at 26 spatially independent community scrapes from 2011 to 2015. We programmed the cameras to record a 60-s video every time motion was detected with a 1-s refractory period. We documented the date, time, and duration of visits by gray foxes, pumas, bobcats, and coyotes to community scrapes. For visits by gray foxes, we also documented the display of: cheek rubbing (where the gray fox rubbed its cheek and chin back and forth on an object), olfactory investigation (noted by its nose being within one head length of the object), and urine scent marking (where the fox squatted or lifted its leg and urinated on an object).

Statistical analyses

We used program *R* version 3.1.1 (R Core Team 2015) for our statistical analyses, and in each statistical test, we considered $p < 0.05$ to be statistically significant.

We first summarized baseline behavior data in order to lay a foundation for understanding unique behaviors in gray foxes. We tested whether gray foxes performed different behaviors when exhibiting cheek rubbing at a community scrape than when they did not exhibit the behavior during a visit. We first used a two-tailed *t*-test (Sokal and Rohlf 1987) to determine if the duration of a visit was

longer when exhibiting cheek rubbing behavior as opposed to none. Due to the lack of normality we first log-transformed the data to meet the assumptions of the *t*-test. We then used 2 × 2 chi-square tests (Sokal and Rohlf 1987) to determine if olfactory investigation and urine scent marking were more frequently displayed during visits when foxes exhibited cheek rubbing as compared to when they did not.

We tested two predictions to distinguish whether gray foxes were more focused on depositing their scent onto the substrate or applying puma scent onto themselves. If gray foxes are cheek rubbing to deposit scent, they should be equally as likely to cheek rub on other objects as they would be on puma individual scrapes. We used a 2 × 2 chi-square test to analyze the selection of each given object compared to puma individual scrapes. Second, if gray foxes aimed to acquire puma scent, we suggest that greater than 50 % of the objects they cheek rub on should be puma individual scrapes. We used a 2 × 2 chi-square test to analyze observed values against expected values of cheek rubbing on puma individual scrapes.

To test whether the exhibition of cheek rubbing behavior was positively correlated with how recently a gray fox had visited a community scrape (depositing scent), or with how recently the puma created an individual scrape (acquiring scent), we used a generalized linear model (GLM) with a binomial link, with fox cheek rubbing or not as our binomial dependent variable, and the number of days since a fox or puma visited as our respective independent variables.

To test whether fox cheek rubbing behavior is exhibited for mate attraction purposes, we used analyses of variance (ANOVA) (Sokal and Rohlf 1987) to determine whether gray fox visitation or cheek rubbing varied among seasons. Seasons were defined as four equal time periods based on the Julian calendar: spring, summer, winter, fall. We tabulated the number of visits and cheek rubbing events in each season, after excluding seasons with <60 days of monitoring, and then log transformed each of the datasets to meet the assumptions of the ANOVA.

To test whether the acquisition of puma scent was for predation avoidance we tested for differences in the relative abundance of the four carnivores at community scrapes. We calculated the relative abundance (RA) of pumas, coyotes, bobcats, and gray foxes at each community scrape as

$$\mathrm{RA} = n \times 100/D,$$

where n is the total number of visits recorded for each species and D is the number of days the community scrape was monitored. We used an ANOVA to test for differences in abundance, using relative abundance as the dependent variable and species as the independent variable, after first log transforming RA to meet the assumptions of the ANOVA. We then performed post hoc Tukey tests to determine where significant differences existed (Sokal and Rohlf 1987).

Results

Overview

We documented gray foxes exhibiting cheek rubbing during 92 out of 903 (10.2 %) visits across our 4 years of observations. When exhibiting cheek rubbing, gray foxes performed a mean of 3.9 (±0.3 SE) back and forth movements, over a mean duration of 11.4 (±1.1 SE) s. The duration of visits when exhibiting cheek rubbing was 37.9 (±2.2) s, significantly longer than the 15.2 (±0.6) s for visits when not exhibiting cheek rubbing ($t_{821} = 10.90$, $p < 0.0001$).

Gray foxes exhibited olfactory investigation at 100 % of visits that included cheek rubbing, significantly more frequently than the 65.2 % at visits that did not include cheek rubbing ($\chi^2_1 = 31.87$, $p < 0.0001$). Gray foxes deposited urine scent marks during 72.5 % of the visits when they exhibited cheek rubbing, significantly more frequently than the 34.4 % of visits that did not include cheek rubbing ($\chi^2_1 = 33.95$, $p < 0.0001$). There appeared to be a sequence of events when cheek rubbing was involved, whereby the fox first investigated the puma's individual scrape, followed by cheek rubbing, then sometimes urination on or near the puma individual scrape (Fig. 3, http://www.momo-p.com/showdetail-e.php?movieid=momo160812uc02a).

Gray foxes performed cheek rubbing on the ground ($n = 12$), a bobcat individual scrape ($n = 1$), and a shrub ($n = 1$), as well as on puma individual scrapes ($n = 78$) (Fig. 4). Across all documented cheek rubbing events, gray foxes performed cheek rubbing on puma individual scrapes 84.7 % of the time, significantly more frequently than on other objects ($\chi^2_3 = 141.53$, $p < 0.0001$), and significantly more than would be predicted by chance ($\chi^2_1 = 23.32$, $p < 0.0001$).

Gray fox cheek rubbing in relation to recent visits by other gray foxes or pumas

The exhibition of cheek rubbing was negatively related to how recently a gray fox had visited ($z_{821} = 2.28$, $p = 0.02$) (Fig. 5a). Visits where gray foxes exhibited cheek rubbing were a mean 13.4 (±1.7 SE) days since a fox visited, while visits where they did not exhibit cheek rubbing were a mean of 11.3 (±0.6) days since a fox visited. The exhibition of cheek rubbing by foxes was positively related to how recently a puma had visited ($z_{817} = 6.52$, $p < 0.0001$) (Fig. 5b). Visits where gray foxes exhibited cheek rubbing were a mean 8.0 (±1.4 SE) days since a puma visited,

Fig. 3 A video showing a typical sequence of events when cheek rubbing was exhibited. The fox first investigates the puma's individual scrape, follows this by cheek rubbing, and then sometimes urinates on or near the puma individual scrape

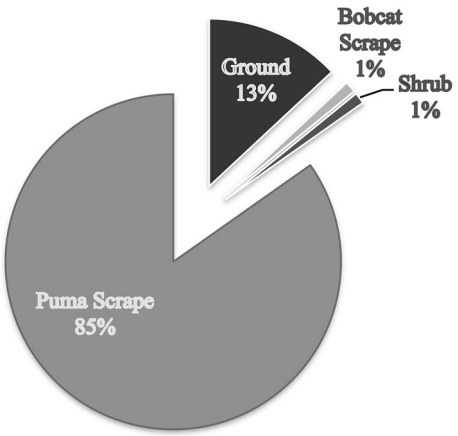

Fig. 4 Percentage of objects gray foxes performed cheek rubbing on different substrates ($n = 92$ cheek rubbing events)

while visits where they did not exhibit cheek rubbing were a mean of 20.5 (±0.7) days since a puma visited. The outlier visit that was 80+ days since a puma visited was the instance of a gray fox cheek rubbing on the shrub.

Seasonality and relative frequency of predator visits

We did not find variation among seasons for either visitation ($F_{3,201} = 1.219$, $p = 0.3$) or cheek rubbing ($F_{3,201} = 0.987$, $p = 0.4$) by gray foxes. Visitation ranged from 3.11 (±0.56 SE) visits in autumn to 3.77 (±0.77) visits in winter. Cheek rubbing ranged from occurring in 0.24 (±0.12) visits in summer to occurring in 0.59 (±0.19) visits in spring.

In testing for predation avoidance, we recorded 1188 visits by pumas (RA = 19.97), 22 visits by coyotes (RA = 0.48), 446 visits by bobcats (RA = 9.51), and 903 visits by gray foxes (RA = 18.19). There was a clear difference in the relative abundance of the four species

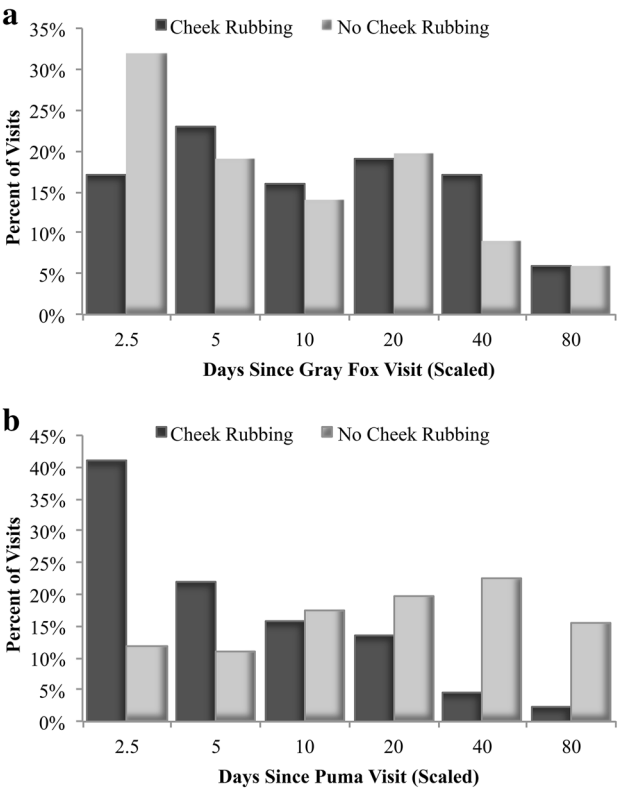

Fig. 5 The relationship between cheek rubbing and recent visits by *gray* foxes (**a**) and pumas (**b**). Visits are scaled to double at each time interval to limit the size of the figure

($F_{3,100} = 84.18$ $p < 0.0001$). Both coyotes and bobcats were less abundant than pumas ($p_{coyote} < 0.0001$, $p_{bobcat} = 0.0014$). Coyotes were also less abundant than gray foxes ($p < 0.0001$), while bobcats were not significantly so ($p = 0.1686$). Gray foxes and pumas were not significantly different in abundance ($p = 0.3143$).

Discussion

Is cheek rubbing by gray foxes for depositing or accumulating scent?

Our results suggest that the adaptive significance behind gray fox cheek rubbing behavior is to acquire scent from puma individual scrapes. Because most scent marking is directed at conspecifics (Roper et al. 1993; Bel et al. 1999; King and Gurnell 2007; Allen et al. 2015a), it was surprising that cheek rubbing by gray foxes had a significant negative relationship with how recently a gray fox had visited. Instead, our results suggest that gray foxes seek out puma community scrapes, and perform cheek rubbing at these areas disproportionately on puma individual scrapes. More specifically, 85 % of cheek rubbing events were performed on puma individual scrapes, and cheek rubbing

had a significant positive relationship to how recently a puma had created the individual scrape. Species are known to use the vocal communications of other species for their benefit (Hughes et al. 2012; Magrath et al. 2015), but this is the first documentation of a species applying the scent from another species onto themselves for their own benefit.

Gray foxes exhibited selection of puma individual scrapes for the performance of cheek rubbing behavior, but mammals often use different forms of scent marking to provide different stimuli (Ralls 1971), and there may be other instances when gray foxes use cheek rubbing to deposit scent in order to communicate with conspecifics. Also, our study was focused on puma community scrapes; if we had recorded gray fox cheek rubbing behavior in other areas, we might have found a higher rate of cheek rubbing on other objects. The next leading object for cheek rubbing after puma individual scrapes was the ground; however, the ground may have been over-represented, as we likely did not document or confirm every previous puma visit or individual scrape, and some instances we attributed to marking on the ground had the visual characteristics of a puma individual scrape. There are many potential reasons for cheek rubbing (e.g., Gosling and McKay 1990), and future research could be performed to determine whether this is the only use of gray fox cheek rubbing or whether they perform cheek rubbing for other purposes and on other objects.

Is cheek rubbing by gray foxes for mate choice or predator avoidance?

Cascading patterns in the abundance of carnivores, particularly among canines, are known to occur (e.g., Levi and Wilmers 2012). Wang et al. (2015) found a site-specific cascading pattern in the activity patterns of pumas, coyotes and gray foxes, while Allen et al. (2015b) found a cascading pattern in the feeding of carnivores at puma kills. We found a similar cascading pattern in the relative abundance of carnivores at puma community scrapes. Cheek rubbing may be a behavioral response used by gray foxes to deter or escape predation from coyotes and bobcats, as smelling like a large carnivore may deter predation events by meso carnivores long enough for the gray fox to escape (e.g., Garvey et al. 2016). This may be a particular advantage for gray foxes, as their main predation avoidance technique is tree climbing (Fritzell and Haroldson 1982) (Fig. 6, http://www.momo-p.com/showdetail-e.php?movieid=momo160812uc03a), and hesitation by a larger predator may give the gray fox time to escape into a tree. The giving up densities (GUP) of prey increase in response to predator scent (Bytheway et al. 2013), and the same may be true of carnivores avoiding larger carnivores. This behavior is likely to be most beneficial against larger predators that are smell-dominant, such as coyotes, and we found that gray foxes visited community scrapes 38 times more frequently than coyotes, suggesting that coyotes avoid community scrapes and puma scent, while gray foxes do not. These findings suggest our hypothesis of cheek rubbing being for predation avoidance is worth follow-up work with studies that can directly test the success of such a tactic.

Fig. 6 A video of a gray fox using its tree climbing ability to escape predation by a bobcat

The lack of seasonality in cheek rubbing behavior and the negative relationship with how recently a gray fox had visited suggest that the acquisition of puma scent was not for mate attraction. The main purposes of scent marking are thought to be for intraspecific territorial marking (Roper et al. 1993; King and Gurnell 2007) and mate attraction (Bel et al. 1999; Allen et al. 2015a). The cheek rubbing performed by gray foxes on puma individual scrapes seems to deviate from this norm, as it appears the gray foxes are accumulating puma scent rather than depositing their own. The lack of seasonality may in part be because gray foxes consort in pairs throughout the year (Fritzell and Haroldson 1982). For example, scent marking is thought to strengthen pair bonds, and cheek rubbing may also serve this purpose. We also did not know the sexes of the foxes performing the cheek rubbing, and this could be a confounding factor, as cheek rubbing is thought to be more prevalent in male mammals (Gosling and McKay 1990). Performing these tests with tagged individuals may shed further light on the pattern, both in discerning patterns for individuals, as well as different sexes.

Conclusions

The mechanisms and importance of scent marking for interspecific interactions are currently underrepresented in the literature. Scent marking is an integral part of the behavioral ecology of many mammals (Mellen 1993; Rostain et al. 2004; Allen et al. 2016), but we have little knowledge of how interspecific scent marking functions. Previous research on interspecific scent marking is sparse, but generally animals are thought to investigate other

species' scent to gain information (Rostain et al. 2004; Li et al. 2013) or avoid predation (Apfelbach et al. 2005; Bytheway et al. 2013). Interspecific vocal communications are used to gain information, find food sources, and avoid predators (Hughes et al. 2012; Magrath et al. 2015), and interspecific use of scent marks may be used for similar functions. The significance of our findings suggest that interspecific scent marking is a potentially rich area of research and an area in need of further research.

Gray foxes cheek rubbing on puma individual scrapes appears to be part of a complex behavioral cascade where a small carnivore acquires scent from a large carnivore to potentially dissuade competition and predation from dominant meso predators. This is the first published study of a subordinate species using the scent of a dominant species to communicate with heterospecifics, and our study suggests that interspecific interactions through scent marking may have important outcomes for community ecology. Interspecific vocal communication can be a mechanism that directly influences the distribution and abundance of species (Goodale et al. 2010), and this behavioral cascade suggests that scent marking could also be a mechanism that impacts the distribution and abundance of species.

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