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Social interactions in a solitary carnivore

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Abstract

In total, 177 of 245 terrestrial carnivores are described as solitary, and much of carnivore ecology is built on the assumptions that interactions between adult solitary carnivores are rare. We employed Global Positioning System (GPS) technology and motion-triggered cameras to test predictions of land-tenure territoriality and the resource dispersion hypothesis in a territorial carnivore, the puma *Puma concolor*. We documented 89 independent GPS interactions, 60% of which occurred at puma kills ($n = 53$), 59 camera interactions, 11 (17%) of which captured courtship behaviors, and 5 other interactions (1 F-F, 3 M-F, and 1 M-M). Mean minimum weekly contact rates were 5.5 times higher in winter, the season when elk *Cervus elaphus* were aggregated at lower elevations and during which puma courtship primarily occurred. In winter, contacts rates were 0.6 ± 0.3 (standard deviation (SD)) interactions/week vs. 0.1 ± 0.1 (SD) interactions/week during summer. The preponderance of interactions at food sources supported the resource dispersion hypothesis, which predicts that resource fluxes can explain temporary social behaviors that do not result in any apparent benefits for the individuals involved. Conspecific tolerance is logical when a prey is so large that the predator that killed it cannot consume it entirely, and thus, the costs of tolerating a conspecific sharing the kill are less than the potential costs associated with defending it and being injured. Puma aggregations at kills numbered as high as 9, emphasizing the need for future research on what explains tolerance among solitary carnivores.

Key words: carnivores, competition, *Puma concolor*, resource dispersion hypothesis, social interactions, tolerance.

In most carnivores, the costs of intraspecific competition outweigh the benefits accrued with group living (Bekoff et al. 1984; Sandell 1989). In total, 177 of the world's 245 terrestrial carnivores and 35 of the 37 wild felids are described as solitary and asocial because they do not cooperatively hunt prey, defend resources, attract mates, or raise their young (Caro 1989; Sandell 1989; Hunter 2011). Ecological theory suggests that solitary carnivores have a better chance than social ones of killing dispersed prey in complex habitats (Seidensticker et al. 1973; Bekoff et al. 1984). Following this theory, much of carnivore ecology is built on the assumptions that interactions between adult solitary carnivores are rare, and only occur during the breeding season or when hostile individuals settle territorial disputes (Kleiman and Eisenberg 1973; López-Bao et al. 2008; Mattisson et al. 2013).

The "land-tenure" hypothesis proposes that solitary carnivores regulate their density through territoriality, temporal avoidance, and chemical communication rather than direct confrontation (Seidensticker et al. 1973; Ferreras et al. 1997; Diefenbach et al. 2006). In a land-tenure system, resident males aggressively defend territories from male conspecifics but overlap with multiple females, and resident females establish sometimes-overlapping territories with sufficient resources to sustain themselves and their dependent young. Resource distributions may further influence the social organization of solitary carnivores at different scales (Wagner et al. 2008; Elbroch et al. 2016b). The resource dispersion hypothesis predicts that higher resource richness, which varies in time and across space, reduces "the resource-based cost of sharing a territory with conspecifics" (Macdonald 1983; Johnson et al. 2002). Resource fluxes may therefore explain temporary associations that do not result in any apparent benefits for the individuals involved (Johnson et al. 2001). For example, tigers *Panthera tigris*, pumas *Puma concolor*, and jaguars *Panthera onca* are solitary, territorial species known to aggregate at kills made by conspecifics and to tolerate each other at close proximity for short time periods (Schaller 1967; Seidensticker et al. 1973; Caro 1989; Guilder et al. 2015).

Historically, researchers relied upon direct observations to study social interactions in animals, or in the case of cryptic carnivores, triangulation of individuals marked with very high frequency (VHF) transmitters to quantify how often individuals were in close proximity to conspecifics (Bekoff et al. 1984). Documenting spatial associations and direct interactions via VHF triangulation, however, is expensive, time-consuming, and suffers biases introduced by the method (Drewe et al. 2012). Global Positioning System (GPS) technology provides researchers the opportunity to monitor animals more continuously, and with less effort (Schauber et al. 2007; Drewe et al. 2012). Social interactions are now being inferred from simultaneous GPS locations of numerous individuals with greater accuracy than was possible with VHF technology, and sometimes long after the associations have occurred (Schauber et al. 2007; Lührs and Kappeler 2013).

The puma is a well-studied, solitary carnivore with the broadest geographic range of any terrestrial mammal in the Western Hemisphere. Pumas range vast territories (mean $571\,km^2$ for males and $210\,km^2$ for females in our study area; Lendrum et al. 2014). Pumas and other felids communicate directly, as well as indirectly via chemical cues to maintain mutual avoidance and advertise mating readiness (Seidensticker et al. 1973; Harmsen et al. 2010; Allen et al. 2015). In 2 long-term puma studies, Seidensticker et al. (1973) and Logan and Sweanor (2001) reported that pumas rarely interacted, avoided each other as a general rule, and that interactions between adults, excepting mating rituals, generally resulted in fitness costs for one if not both pumas (e.g., mortality). Male pumas are considered a danger to females outside breeding, and expected to commit infanticide when they encounter females with kittens (Logan and Sweanor 2001; Packer et al. 2009). In their long-term project in New Mexico, Logan and Sweanor (2001) assessed 269 paired puma associations determined from location data from individuals marked with VHF transmitters. In total, 75% of male–female (M-F) puma associations were suspected to be driven by mating rituals, and 29% of male–male interactions resulted in the death of 1 puma (Logan and Sweanor 2001).

We employed GPS collar technology and motion-triggered camera data to test predictions of land-tenure territoriality and the resource dispersion hypothesis in asocial carnivores (Elbroch et al. 2016b), as well as the behavioral assumptions of solitary carnivores as described by Sandell (1989). Based on the literature, we hypothesized that puma interactions would be rare, that male–female interactions would outnumber any other type of interaction, and that courtship rituals would explain most interactions (Kleiman and Eisenberg 1973; Logan and Sweanor 2001; López-Bao et al. 2008). Pumas, however, kill more meat than they eat (Elbroch et al. 2014a), providing opportunities for co-feeding with conspecifics and potential unexpected sociality or breaches in territorial behaviors as predicted by the resource distribution hypothesis (Elbroch et al. 2016b). To test our hypotheses, we quantified first-ever contact rates for pumas, quantified the proportion of interactions recorded by cameras in which pumas exhibited courtship (M-F), and determined the proportion of conspecific interactions that occurred at food sources.

Materials and Methods

Study area
Our puma study covered $2,300\,km^2$ of the Southern Yellowstone Ecosystem (SYE), inclusive of Grand Teton National Park, the National Elk Refuge, and the Bridger-Teton National Forest north of Jackson, Wyoming. Elevations in the study area ranged from 1,800 m to >3,600 m. The area was characterized by short, cool summers during which prey are widely dispersed and long winters with frequent snowstorms during which elk *Cervus elaphus* form large aggregations at lower elevations (Elbroch et al. 2013; Elbroch et al. 2016b).

Puma capture and collar programming
We captured pumas during winter months from 2012 to 2015, when we employed trailing hounds to force pumas to retreat to a tree where we could safely capture them. Pumas were fitted with a GPS collar (Lotek Globalstar S or Iridium M, Newmarket, Ontario; Vectronics Globalstar GPS Plus, Berlin, Germany). Our capture protocols adhered to the guidelines outlined by the American Society of Mammalogists (Sikes et al. 2011) and were reviewed by the Jackson Institutional Animal Care and Use Committee (Protocol 027-10EGDBS-060210). All GPS collars were programmed to acquire simultaneous location data every 2 h (12 times per day).

Puma interactions and contact rates
Following guidelines established in the literature for detecting spatial associations in solitary felids (Elbroch et al. 2014b; López-Bao et al. 2014), we defined "GPS interactions" as simultaneous location data for any 2 individual adult pumas wearing GPS collars at a distance of ≤200 m from each other, between April 2012 and March 2015. Individuals needed to separate at >200 m from each other for >24 h before we counted their reunion as a "new" GPS interaction. We defined "camera interactions" as footage of multiple pumas caught on motion-triggered video cameras or handheld video cameras. As with GPS interactions, individuals needed to separate from each other (not be recorded at the same kill) for >24 h before we counted their reunion as a "new" camera interaction. We defined "other interactions" as those we documented opportunistically through other means, primarily through discovering multiple pumas together during capture events, or when tracking a puma wearing a collar that happened to be with an unmarked animal.

We knew we did not mark every puma in the population and that the different types of interactions described above would capture interactions with different success. Therefore, we quantified conservative, minimum weekly contact rates for marked pumas for 2 seasons by summing GPS interactions + camera interactions unaccounted for with GPS data (e.g., interactions with unmarked individuals) + other interactions, and then we divided by the number of days each individual was monitored in that season and scaled to 1 week. We defined seasons following well-established elk migration dates in the study area: "winter" from 1 December of 1 year through 31 May of the next year, and "summer" as 1 June through 30 November of the same year (Elbroch et al. 2013).

Identifying puma kills, social interactions at kills, and courtship behaviors
GPS data acquired by puma collars were uploaded to Globalstar satellites 6 times per day or once per day to Iridium satellites. Upon retrieval, we displayed location data in ArcGIS 10.0. (ESRI, Redlands, CA), and following protocols for studying puma foraging (Elbroch et al. 2014a), we visually identified aggregated GPS points in which ≥2 locations spanning ≥4 h of time were within 150 m of each other. Researchers transferred puma location data to handheld GPS units to guide them in the field, and we systematically searched aggregated locations to locate and identify prey remains. The state of prey remains, presence and location of bite marks, and body parts

consumed were used to determine whether the puma had killed the animal or was scavenging. When pumas were still feeding on a carcass, we placed motion-triggered video cameras with sound capabilities (Bushnell Trophy Cam HD Max, Bushnell Outdoor Products, Overland Park, KS, USA) to record 60-s videos of activity, with a 30-s delay between videos.

We documented multiple pumas at puma kills in 2 ways: 1) "GPS interactions" at puma kills we verified through field investigations of aggregated GPS location data, and 2) through camera interactions between marked or unmarked pumas at puma kills. Videos captured of multiple pumas were watched carefully in our office to assess whether either puma exhibited courtship behaviors. Courtship behaviors were defined as including physical rubbing between pumas or breeding vocalizations, such as caterwauling. We employed 2-proportion z-tests to compare whether the proportion of M-F or F-F GPS interactions at food resources were different from those unassociated with puma kills.

Results

Pumas, contact rates, and conspecific tolerance

Between April 2012 and March 2015, we marked 16 adult pumas with GPS collars, 12 of which overlapped in space and were included in our analyses of frequency of interactions; 3 of these pumas were killed soon after they were included in the study: 1 poached (F57), 1 suspected poisoned (M21), and 1 killed by a conspecific (F59). We documented 89 independent GPS interactions, 60% of which occurred at puma kills ($n = 53$). Individual collar performance was variable; overall, mean GPS acquisition was $83 \pm 11\%$ (SD), which may have reduced opportunities to document GPS interactions. As a whole, 52 GPS interactions were M-F, 33 were F-F, and 4 were M-M. There was no difference in the proportion of M-F ($z = 0.852$, $P = 0.395$) or F-F ($z = 0.671$, $P = 0.503$) interactions associated with puma kills versus interactions unassociated with food resources.

We documented 59 camera interactions (32 F-F, 27 M-F; Figure 1; Supplementary Video 1), 11 (17%) of which captured courtship behaviors (Supplementary Video 2), and 5 other interactions (1 F-F, 3 M-F, 1 M-M). In total, 24 of 59 camera interactions were unaccounted for by GPS interactions. When combining all methods and removing redundant data, we found support for our hypothesis that interactions would predominantly occur between males and females: we documented a total of 65 M-F, 48 F-F, and 5 M-M interactions. Mean minimum weekly contact rates were 5.5 times higher in winter, the season when elk were aggregated at lower elevations and during which puma courtship primarily occurred, as defined in Elbroch et al. (2015) (Figure 2). In winter, contacts rates were 0.6 ± 0.3 (SD) interactions/week versus 0.1 ± 0.1 (SD) interactions/week during summer (Table 1).

The duration of interactions at puma kills was 25.4 ± 27.8 h (SD) (range 2–121 h), whereas interactions unassociated with food sources were 8.7 ± 18.2 h (SD) (range 1–76 h). We were only able to determine 2 cases in which an incoming puma displaced the puma that had made the kill; more typically, the pair alternated feeding at the carcass. Zero M-M interactions resulted in mortality, but 2 M-F interactions resulted in the death of the females. We classified the first event as predation rather than intraspecific strife. M68, a 2-yr old sub-adult male puma that we believe had not eaten for more than 5 weeks because we did not find prey remains at any place where GPS locations were aggregated; his last confirmed prey was a porcupine and he may have suffered injuries that limited his mobility

Figure 1. Characteristic hissing and posturing of adult female pumas *Puma concolor* meeting at a carcass.

(Elbroch et al. 2016a). M68 encountered F59, an 18-month subadult female puma, away from a food resource and killed her. He lay atop her carcass and consumed her over the following 4 days. Visually, we confirmed his starving status—all his ribs, pelvis, and leg bones were showing through his coat.

We classified the second M-F interaction resulting in mortality as intraspecific strife. F51, a resident female with 2 7-month old kittens, encountered and attacked M85, a mature male wandering into previously held territory by an adjacent male recently killed by a hunter. Evidence (e.g., tracks in the snow) did not suggest that M85 threatened F51 or her kittens, but we suspect that the defense of her offspring triggered the attack. M85 ultimately killed F51.

Kittens were present at 60% ($n = 56$) of incidents of F-F and M-F co-feeding (Supplementary Video 3). On 5 occasions, we documented 3 adult pumas feeding together. In the first 2 instances, M21 fed with F61 and F51 and their 4 kittens that he sired (7 pumas total). In the third, M29 fed with F61 and F51 and their 4 unrelated kittens sired by M21 (7 pumas total). In the fourth, courting pair M85 and F108, fed with F49; neither female had kittens at the time. In the fifth, 3 adult females without kittens fed together. Puma aggregations at puma kills numbered as high as 9, inclusive of kittens. We also documented a case of 3 pumas displaying courtship behaviors together. F108, F47, and M85 spent several days traveling together, during which the females alternately mated with the male, while the other lay close by (Supplementary Video 4).

Discussion

Our research provided evidence that non-cooperative, solitary species associate with conspecifics with regularity (Leyhausen 1979; Sandell 1989), and perhaps with predictability as well. Puma interactions predominantly occurred at food resources during the time period when prey were aggregated and courtship rituals were occurring (Elbroch et al. 2016b). These observations contradicted earlier research on solitary carnivores that recorded few F-F associations and interpreted M-F associations as predominantly driven my courtship (e.g., Logan and Sweanor 2001). Further, these revelations challenge us to reconsider current assumptions about how social behaviors influence animal distributions, territoriality, intra- and inter-specific competition, and disease transmission between conspecifics (Linnell and Strand 2000; Ji et al. 2005; Hamede et al. 2009).

The preponderance of interactions at food sources supported the resource dispersion hypothesis in a solitary carnivore, as predicted
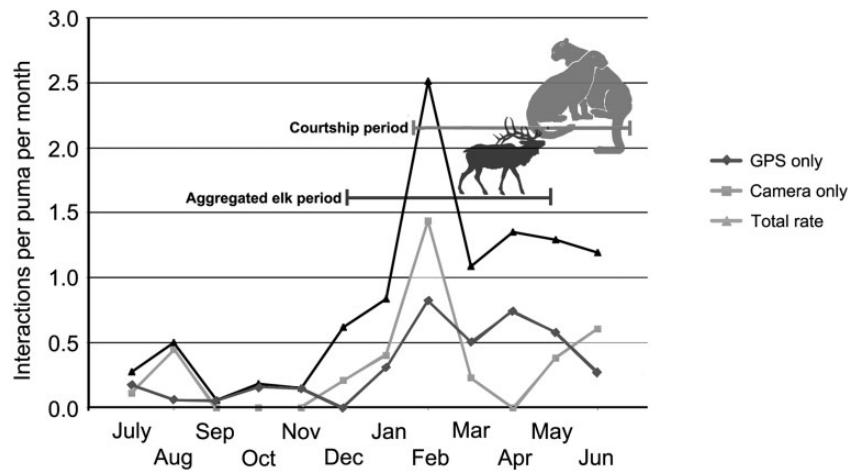
Figure 2. Total interactions per month per marked puma *Puma concolor*, as determined with GPS data only, and camera data only. GPS and camera data are reported separately to emphasize the differences in what they captured. The time periods associated with aggregated elk *Cervus elaphus* and puma courtship (Elbroch et al. 2015) are overlaid in dark gray and light gray, respectively.

Table 1. Individual puma interactions and minimum weekly contact rates for 2 seasons (F = female and M = male)

Cat ID	Season	Days monitored	GPS interactions	Camera interactions	Other	Total interactions	Contact rate
M29	Winter	215	25	15	–	40	1.3
M21	Winter	30	1	–	1	2	0.5
F57	Winter	36	4	–	–	4	0.8
F109	Winter	360	16	6	–	22	0.4
F51	Winter	334	23	8	–	31	0.6
F61	Winter	483	23	7	1	31	0.4
M85	Winter	325	22	7	1	30	0.6
M68	Winter	172	7	4	–	11	0.4
F49	Winter	335	14	7	–	21	0.4
F59	Winter	15	1	–	1	2	0.9
F108	Winter	109	–	9	–	9	0.6
F47	Winter	473	20	16	–	36	0.5
M29	Summer	171	1	1	1	3	0.1
F109	Summer	186	1	–	–	1	0.0
F51	Summer	366	4	2	–	6	0.1
F61	Summer	366	5	4	–	9	0.2
M85	Summer	183	4	–	1	5	0.2
F49	Summer	183	2	–	–	2	0.1
F47	Summer	366	5	–	–	5	0.1

by Elbroch et al. (2016b), in which researchers assessed heterogeneous hunting opportunities as an explanation for home range overlap. Conspecific tolerance is logical when a prey is so large that the predator that killed it cannot consume it entirely, and thus the costs of tolerating a conspecific sharing the kill are less than the potential costs associated with defending it and being injured (MacDonald 1983). Tolerance may also be explained by kinship (Hamilton 1964; Elbroch et al. 2016b), but previous research in our system indicated that puma associations were between the least-related individuals (Elbroch et al. 2014b).

Prey size may also influence tolerance. If so, the fact that local puma diets are almost exclusively large elk in winter (Elbroch et al. 2013) may explain the higher frequency of interactions in that season. Further, if tolerance only occurs at large carcasses, reciprocal tolerance among pumas might be a strategic foraging strategy wherever pumas expend significant energy to kill prey many times their size.

Our methods were not designed to address the question as to whether pumas exhibited behaviors that challenge their description

as a "solitary" carnivore, although we did gain some insights into this question. Conservatively, pumas in our study interacted an average of 26 times per year with other adults, which is a very small number when one considers the potential number of days in which pumas could interact in a calendar year. Sandell (1989) emphasized that solitary is not the same as non-social (Sandell 1989) and that all solitary felids are social to some degree (Leyhausen 1979). Primatology also offers useful definitions applicable to solitary carnivores: Among primates, "solitary" species are those that exhibit asynchronous movements with conspecifics, and forage alone (Kappeler and van Schaik 2002), as is typical of pumas and many other solitary carnivores. Further, primatologists recognize that solitary "does not imply that they [solitary species] do not maintain social relations" (Kappeler and van Schaik 2002). Thus, the frequency with which pumas interacted with conspecifics was not enough to challenge the puma's status as a solitary species.

Let us address each of Sandell's (1989) solitary behaviors presented in the Introduction: 1) We did not document any instances of

cooperative foraging (e.g., hunting) between pumas. 2) We did not document any cooperative mating strategies among pumas. We did, however, observe 2 females with a single male. Nevertheless, the females did not appear to be working together to court the male, but rather exhibiting tolerance of a conspecific at a "resource" (a breeding-age male). 3) We did not document any instances in which pumas cooperatively defended resources. 4) We did not document cooperative breeding among pumas (Lukas and Clutton-Brock 2012), such as cooperatively raising offspring. We did, however, document adult pumas exhibiting tolerance of unrelated females with kittens scavenging at his or her kill. For example, F51 and F61, a pair of unrelated adult females with overlapping home ranges (Elbroch et al. 2016b), both with offspring, co-fed at 9 deer and elk carcasses in 2012. In total, 3 carcasses were killed by F51, and 6 by F61. When the pair stopped associating at kills, F61 adopted 1 of F51's offspring (F88) and provided for her for an additional 4 months before F88's dispersal at 14 months of age.

Conspecific tolerance among solitary carnivores at food sources is an important topic of research. Next steps include determining whether variation in prey availability, carnivore density, or prey size influence the frequency of tolerance, or whether tolerance might be better explained by kinship or reciprocity. Motion-triggered cameras combined with GPS technology may provide researchers the tools to study tolerance and other cryptic behaviors previously very difficult to observe.

Supplementary material

Supplementary material can be found at http://www.cz.oxfordjournals.org/.

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