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BEHAVIORAL ECOLOGY

Adaptive social strategies in a solitary carnivore

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Cost-benefit trade-offs for individuals participating in social behaviors are the basis for current theories on the evolution of social behaviors and societies. However, research on social strategies has largely ignored solitary animals, in which we assume that rare interactions are explained by courtship or territoriality or, in special circumstances, resource distributions or kinship. We used directed network analysis of conspecific tolerance at food sources to provide evidence that a solitary carnivore, the puma (*Puma concolor*), exhibited adaptive social strategies similar to more social animals. Every puma in our analysis participated in the network, which featured densely connected communities delineated by territorial males. Territorial males also structured social interactions among pumas. Contrary to expectations, conspecific tolerance was best characterized by direct reciprocity, establishing a fitness benefit to individuals that participated in social behaviors. However, reciprocity operated on a longer time scale than in gregarious species. Tolerance was also explained by hierarchical reciprocity, which we defined as network triangles in which one puma (generally male) received tolerance from two others (generally females) that also tolerated each other. Hierarchical reciprocity suggested that males might be cheating females; nevertheless, we suspect that males and females used different fitness currencies. For example, females may have benefited from tolerating males through the maintenance of social niches that support breeding opportunities. Our work contributes evidence of adaptive social strategies in a solitary carnivore and support for the applicability of theories of social behavior across taxa, including solitary species in which they are rarely tested.

INTRODUCTION

Determining fitness benefits for individuals participating in social behaviors is fundamental to understanding the evolution of animal social organization (1–4). For example, animals benefit through direct reciprocity, during which individuals share resources with conspecifics that reciprocate in kind, or generalized reciprocity through which they share resources with one individual but receive benefits from another that compensate for the costs of their behaviors (4–7). Gregarious animals that interact frequently with each other also use cooperative social strategies to form societies that share diverse benefits, such as predator avoidance through dilution, group defense against threats, cooperative foraging, and shared parenting (2–4, 8). In contrast, solitary species derive greater fitness benefits from avoiding other members of the same species and therefore exhibit limited sociality (9). Solitary animals are defined as those that exhibit asynchronous movements with conspecifics (3), and they are characterized by such infrequent, short social interactions that we assume they do not develop adaptive social strategies (10). Consider terrestrial carnivores, a group of ecologically important taxa (11) of which 179 of 247 species are solitary and suffer costs of intraspecific competition, including reduced access to shared resources and greater difficulty in stalking prey in complex habitats in which it is more difficult to be stealthy (12–15). Instead of living with conspecifics, solitary carnivores maintain separate territories or temporal avoidance, except during courtship or settling territorial disputes (14, 16).

Ecologists generally assume that rare social interactions among solitary species are explained by three simple tenets: resource dispersion, animal spatial distributions, or kinship. The resource dispersion hypothesis predicts that resources are heterogeneous in space and that resource clumping can explain spatial overlap or temporary associations between typically solitary animals (8, 17, 18). The land-tenure hy-

pothesis, characterized by range-guarding polygyny (4), predicts that the spatial organization of solitary carnivores is also driven by resources: Female solitary carnivores establish sometimes-overlapping territories of a size sufficient to feed themselves and their dependent young and also supplement any overlapping males, whereas male solitary carnivores maintain large, exclusive territories overlapping numerous females to protect mating opportunities (9, 14, 19–21). Last, kinship theory predicts that animals exhibit higher tolerance for related conspecifics, because tolerance is then a selfish investment in an animal's own genetic lineage (8, 22). Many carnivores do exhibit localized matrilineal lineages (9), because many female offspring remain philopatric to their natal ranges and establish territories overlapping with or very near their mothers. Kinship is thus linked with the spatial organization of territories, and territories are established on the basis of the distribution of available resources. In summary, theory predicts that solitary carnivores interact infrequently, but when they do, it is likely with neighbors that are also relatives in areas where resource richness reduces the costs of intraspecific competition.

Pumas are a widespread solitary felid in the Western Hemisphere and a species that exemplifies range-guarding polygyny and assumptions about solitary animal social behaviors (9, 18, 23). Pumas also exhibit two traits shared by many carnivores that suggest that they hold potential for more complex social strategies than is currently expected for solitary species. First, pumas regularly kill prey many times their size and difficult to consume alone. Excess food reduces the costs associated with being close to conspecifics, thus increasing opportunities for social interactions and the development of more complex social strategies (8, 13, 21). Second, pumas live long lives in relatively stable territories, providing opportunities for repeated interactions with neighbors over time. The opportunity for repeated interactions is a critical assumption in how complex social strategies, such as cooperation, might develop (7). However, until the advent of Global Positioning System (GPS) technology, interactions between cryptic species like pumas were difficult to quantify.

We used GPS location data from marked pumas (*Puma concolor*) and motion-triggered video cameras to gather data on puma social

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interactions at puma kills in northwest Wyoming (24). We focused on interactions at food resources for two reasons: (i) It was shown that pumas in our study system interacted most often at food sources (24), and (ii) these interactions provided us the opportunity to assign a “giver” and “receiver” to each interaction, a distinction necessary to test for adaptive social strategies such as reciprocity. In the case of our research, puma A (giver) exhibited tolerance of puma B (receiver) if puma B visited a kill made by puma A, and they coted at the carcass. Then, we used directed network analysis, including exponential random graph models (ERGMs) (25), to test whether a puma’s tolerance for conspecifics was explained merely by ecological factors (for example, the distribution of resources and associated puma spatial overlap) or whether complex social strategies (for example, reciprocity) also explained resource sharing.

On the basis of assumptions that solitary carnivores interact infrequently and do not exhibit complex social strategies, we established two null hypotheses: We hypothesized (i) that our network would include disconnected individuals that did not tolerate other pumas and in turn were not tolerated by other pumas and (ii) that network connections between pumas would be explained by kinship or the spatial overlap of the individual pumas involved [previous research in our study system showed that spatial overlap among pumas was explained by resource distributions (18)]. We also tested three alternative hypotheses and whether conspecific tolerance might be explained by adaptive social behaviors: We hypothesized (i) that tolerance would be explained by direct reciprocity between pumas; (ii) that tolerance would be explained by hierarchical reciprocity among pumas, which we defined as network triangles consisting of three individuals in which one received greater benefits through social interactions than the remaining two (26); and (iii) that tolerance would be explained by generalized reciprocity among pumas (27), an egalitarian system that, in terms of network analysis, was characterized by network triangles consisting of three individuals, each of which would tolerate and would be tolerated by at least one other member of the triangle. Finding evidence for adaptive social strategies in a solitary carnivore would challenge current assumptions about the social behaviors of solitary species and provide support for the applicability of theories governing social behaviors across all taxa, including solitary species in which adaptive social behaviors are rarely tested (21).

RESULTS

Pumas and instances of tolerance

Between April 2012 and March 2015, we marked 16 independent sub-adult and adult pumas with GPS collars, 11 of which overlapped in space and were included in our analyses. We also documented two unmarked pumas at kills made by marked pumas that overlapped with our focal group (UncF1 and UncF2), suggesting that we had successfully marked 85% of the resident pumas in our core study area. We included 13 pumas (11 marked and 2 unmarked but identifiable) in our network analyses of tolerance at food resources (Table 1), establishing the opportunity for 156 dyadic interactions in the network. We recorded 81 instances of tolerance, and social interactions at carcasses lasted on average 25.4 ± 27.8 hours (SD) (range, 2 to 121 hours).

Network analyses

Our network contained four males and nine females (Table 1). Genetic relatedness between interacting pumas was low (mean relatedness, 5%). At least one instance of tolerance was observed in 26% of the pairs, and the maximum number of instances of tolerance between two pumas was

12 (Fig. 1). We conducted a bivariate correlation comparison (Table 2) between the number of edges (cases of tolerance) and the attributes of puma dyads that suggested that older pumas exhibited tolerance more often than young pumas and that male pumas benefited from tolerance more often than they exhibited tolerance. It also suggested that the greater the spatial overlap between two pumas, the more likely they were to be connected in the network. This descriptive analysis did not indicate any correlation between kinship and tolerance.

We used conditional uniform graph (CUG) tests (28) to determine whether structures in our puma network were found more or less often than would be expected by chance; we did this by comparing network structures established from field observations to network structures established through simulations made with the same number of nodes and edges and their resulting frequency distribution. The results of our CUG tests (Table 3) revealed much higher levels of direct reciprocity and hierarchical reciprocity in the empirical network than expected by chance ($P < 0.001$). The large empirical values and low P values for modularity and clustering reflected “communities” in the larger network, within which there were greater frequencies of tolerance, and across which there were less frequent cases than would be expected by chance (Table 3). Our community detection analysis identified two communities, corresponding to the spatial boundaries of territorial male home ranges (M29 and M85) (Fig. 1 and Table 1). Finally, the provisioning of tolerance was marginally more concentrated than expected by chance, whereas the receiving of tolerance was not; this indicated that although some pumas exhibited tolerance much more than others, the receiving of tolerance was evenly distributed across the network.

Next, we used ERGMs (25) to better tease apart the effects that would support our null (spatial overlap and kinship) versus alternative hypotheses (various forms of reciprocity). Despite the challenges posed by the interdependence of observations in a network context, ERGMs provide unbiased estimates of drivers of network connections (for example, tolerance) while controlling for all other included effects, analogous to multiple regression. We estimated both a binary ERGM (that is, has puma A ever tolerated puma B?) and a count-edge ERGM (that is, how many times has puma A tolerated puma B?) modeled as a Poisson distribution. Count-edge models captured more of the variance in tolerance than the binary analysis because many dyads exhibited tolerance for each other multiple times. For example, neighboring females (F51 and F61) exhibited tolerance 11 times between them.

The ERGM estimates (Table 4) provided additional evidence of direct and hierarchical reciprocity, even while accounting for the spatial distribution of pumas and other effects. Direct reciprocity was consistently one of the strongest effects in all analyses: On the basis of the exponentiation of slope coefficients from the binary ERGM, if puma A tolerated puma B, then puma B was 7.7 times more likely to tolerate puma A. There was also strong evidence for hierarchical reciprocity (transitivity). These transitive triads tended to be network triangles formed of two females that tolerated each other and the same male: The odds that a pair would exhibit tolerance for each other was 2.5 times greater if both individuals tolerated the same third. Our results also suggested that puma pairs with overlapping territories exhibited tolerance more than nonoverlapping pairs and that males were more likely to receive tolerance (in-degree) and less likely to exhibit tolerance at their own kills (out-degree) than females. However, spatial overlap and sex effects were only significant in the count-edge model, which retained enough information about the frequency of social interactions to differentiate these exogenous processes. We did not find support for kinship or generalized

Table 1. Puma attributes. Individual pumas ($n = 13$) and their attributes, including age, weight, and the community cluster to which they belonged (1, 2), as identified through our analyses, followed by their network attributes. F, female; M, male; NA, not applicable.

Puma ID	Age (months)	Weight (kg)	Community	Outgoing tolerance	Receiving tolerance	Betweenness centrality	Eigenvector centrality
M68	22	55	1	3	2	30	0.08
M29	54	70	1	2	18	28	0.02
M21	72	75	1	0	2	0	0
F57	105	40	1	2	0	0	0.02
F109	84	40	1	5	6	43	0.06
F61	82	45	1	18	3	0	0.18
F51	70	48	1	14	11	26	0.12
UncF2	NA	NA	1	0	2	0	0
M85	84	74	2	4	18	10	0.35
F49	72	43	2	11	5	50	0.53
F108	76	45	2	2	7	0	0.1
F47	84	47	2	20	3	3	0.73
UncF1	NA	NA	2	0	4	0	0

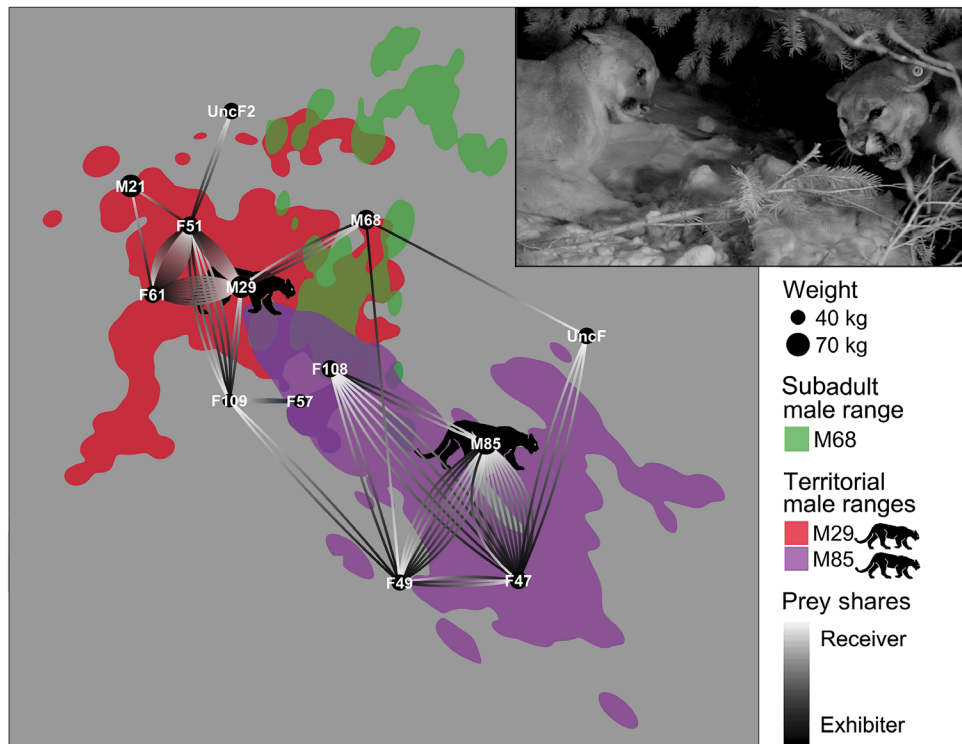


Fig. 1. Puma network. Graphical representation of the network overlaid the territories of resident and subadult male pumas. M29 and M85, territorial males represented with puma icons, delineate the spatial extent of the two communities identified through our analysis. Inset: An interaction between two adult females (UncF2 and F51) over the prey killed by F51.

Table 2. Correlations between frequency of tolerance and puma characteristics. Here, we present Pearson correlation coefficients and their associated P values based upon a two-tailed null hypothesis of no correlation (in parentheses). Age, weight, and sex are correlations between an individual puma's attributes and their tolerances with all other pumas ($n = 13$); spatial overlap and relatedness are dyadic attributes correlated with the number of tolerances for that pair ($n = 156$). Spatial overlap is the proportion of the home range of the puma exhibiting tolerance that is overlapped by the home range of the puma receiving tolerance. Relatedness is a single value because it represents the dyadic relationship between two pumas in each interaction rather than the attributes of each puma. Larger positive values indicate a positive correlation, and larger negative values indicate a negative correlation. Values close to 0 indicate that the variables were not correlated.

	Exhibiting tolerance (out-degree)	Receiving tolerance (in-degree)
Age (months)	0.213 ($P = 0.48$)	-0.09 ($P = 0.77$)
Weight (kg)	-0.283 ($P = 0.35$)	0.573 ($P = 0.04$)
Male (versus female)	-0.391 ($P = 0.19$)	0.442 ($P = 0.13$)
Spatial overlap	0.485 ($P < 0.01$)	0.08 ($P = 0.32$)
Relatedness	-0.011 ($P = 0.89$)	

reciprocity (cyclicality) explaining patterns of tolerance in the network; the effects of kinship were too noisy to draw inferences.

Aggression during food sharing

We placed cameras at 242 active puma kills and used 48 camera interactions to describe the overall aggression between pumas actively food sharing. Puma interactions were characterized by short, intensive exhibitions including physical posturing (for example, elevated heads, stiff front legs, and flattened ears) and auditory communication (for example, hissing and growling), followed by peaceful bouts of co-feeding or alternate feeding while the other puma rested nearby. Female behavior included hisses and growls and, occasionally, swats, charges, or physical contact (movies S1 and S2). By contrast, males typically approached kill sites of other pumas tentatively and in a hunched position that minimized their size (movie S3). Females were more aggressive than males ($F_{1,8.3} = 9.91$, $P = 0.01$). Female mean aggression was 2.76 ± 0.24 (SE), and male aggression was 1.19 ± 0.44 (SE).

We used 29 camera interactions between genotyped pumas to assess the influence of kinship and dyad type (male-female or female-female) on aggression during food sharing. Neither kinship ($F_{1,6.8} = 1.04$, $P = 0.34$) nor dyad type ($F_{1,5.9} = 1.92$, $P = 0.34$) influenced aggression.

DISCUSSION

We used directed network analyses to reveal sophisticated social behaviors and social organization in a solitary carnivore, including direct reciprocity and hierarchical social structures typically considered the sole dominion of social animals. In general, we did not find support for our null hypotheses established by the current literature on solitary animals. Pumas exhibited prolonged tolerance at food sources, and every puma in our focal area participated in the network, challenging us to reconsider our assumptions about the social strategies of diverse solitary species. Contrary to our hypotheses, kinship did not explain

Table 3. Results of CUG tests. Results of our CUG tests, with empirical values of network statistics and the probability of observing a greater value in a random network of the same size and density.

	Empirical value	Probability versus simulations
Direct reciprocity	0.23	<0.001
Hierarchical reciprocity (transitivity)	0.38	<0.001
Modularity	0.38	0.014
Clustering	0.40	0.019
Exhibiting tolerance centralization	0.26	0.060
Receiving tolerance centralization	0.18	0.299

tolerance, and spatial overlap was an explanatory variable of secondary importance, functioning within the larger constraints imposed by the social organization around territorial males.

Puma tolerance for conspecifics at large carcasses was best explained by direct reciprocity, establishing a benefit to individuals that participated in the network. Many researchers believe that animals lack the cognitive capacity for recalling experiences and strategic thinking required to exhibit reciprocity, but there is increasing evidence of its existence in wild animals (6, 26, 29). Direct reciprocity proves a stable cooperative strategy when the costs of sharing are low, there is a high chance of repayment, and animals are likely to interact multiple times, allowing them to base their decisions to participate in social interactions upon experience rather than indirect knowledge (4, 7, 30). In our study system, social interactions among pumas met each of these requirements. To begin with, excess food reduces the costs of reciprocity and creates opportunities for sociality in normally solitary species (8, 13). Carnivores that kill large prey, which are difficult to consume alone, temporarily experience excess resources, as do those species that suffer rapid kleptoparasitism by competitors and so rarely finish the prey they procure. Under these scenarios, there may be fitness benefits to supporting conspecifics over competitive scavengers, as has been shown in social carnivores (31). For example, reciprocity may serve to build social relationships that reduce the potential for dangerous physical contests between overlapping pumas. Reciprocal tolerance may also increase individual fitness by reducing the frequency that individuals need to hunt large, dangerous prey, thus mitigating both energy expenditures associated with hunting and associated risks of injury. Local puma diets in our study, case in point, were almost exclusively elk in winter (24), a large prey difficult to consume for a single puma. Tigers (*Panthera tigris*), jaguars (*Panthera onca*), wolverines, and brown bears (*Ursus arctos*) are also solitary, territorial species known to aggregate at large kills made by conspecifics (13, 32–35), which also suggests the potential for adaptive social strategies in these species.

Territorial male behavior provided both physical and hierarchical structure to puma linkages in the network. Pumas exhibited more frequent interactions within network clusters delineated by male territories (Fig. 1), indicating that our population of solitary pumas was in fact a

Table 4. Results of our ERGMs. Coefficients are analogous to logistic regression coefficients (log-odds change per unit increase in the associated predictor). SEs of the estimates are in parentheses. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

	Binary edges	Valued edges
Land-tenure and kinship hypotheses		
Relatedness	2.22 (2.09)	0.25 (0.68)
Spatial overlap	1.44 (1.09)	0.88* (0.37)
Male receiving	1.02 (0.65)	0.42** (0.16)
Male sharing	-0.67 (0.47)	-0.68** (0.26)
Social behavior hypotheses		
Direct reciprocity	2.04* (0.83)	0.78* (0.31)
Hierarchical reciprocity (transitivity)	0.91* (0.46)	0.28* (0.14)
Generalized reciprocity (cyclicality)	-0.18 (0.36)	-0.09 (0.14)
Basic network attributes		
Density	-4.02*** (0.91)	0.48* (0.22)
Any shares		-4.42*** (0.42)
Even-distribution receiving	2.59 (1.52)	
Even-distribution sharing	-0.45 (0.97)	

collection of smaller social communities defined by male territories. Individuals within these communities interacted frequently with each other and less often with others in neighboring communities. Territorial males also structured social interactions among all pumas, a finding that holds immediate ramifications for numerous species suffering the diverse effects of trophy hunting by humans. Human hunting is typically selective of specific age or sex classes, which influences population demography and the heritability of specific traits over time (36, 37). Trophy hunting of carnivores may also increase human-carnivore conflict (38) and disrupt a species' socio-spatial organization. For example, brown bears suffer social disruption for up to 2 years following the selective hunting of mature males in the population (39); remaining males shift their home ranges following the death of a neighboring male and increase the infanticide of cubs they encounter in their expanded territory (39, 40). Similar social disruption has been suggested for pumas under heavy pressure from trophy hunting (41). In hunted populations, male pumas exhibit larger home ranges that overlap more with neighboring males, increasing the potential for male-male fighting (42).

Males also consistently benefited from tolerance more than females, and females consistently provided tolerance more than males, suggesting that males might be cheating in a cooperative system of reciprocity (43). Because all males rather than individual males exhibited this pattern, we believe that it was more likely that males and females experienced the costs and benefits of exhibiting and receiving tolerance differently (4, 44) or used mixed currencies for fitness. For example, females that tolerated males may have benefited through the development of relations with the resident male or the maintenance of social niches (45) that provided them better breeding opportunities. Female-

male relations may be critical in a range-guarding polygyny system, in which resident females sometimes lack choice.

In summary, puma social behaviors in our study system were diffused over space (mean puma territories, 571 km² for males and 210 km² for females) (46) and time (in winter, pumas interacted with conspecifics every 11 to 12 days) (24). Nevertheless, pumas in our study system also proved more frequently social and more strategically social than predicted based on current assumptions about solitary species. Theories on the evolution and adaptive significance of social behaviors were developed from research on gregarious, group-living animals (21), and our work provides support for their application across taxa, inclusive of solitary species in which they have rarely been tested. Pumas in our study system met several criteria for potential sociality presented in current theories of social behaviors. However, pumas also exhibit great dietary breadth and variable densities across their range in North America and South America; further comparisons are needed to determine whether what we discovered in our study system is applicable across puma populations of different densities or with different prey assemblages (for example, small prey versus large prey and migratory prey versus stationary prey).

MATERIALS AND METHODS

Study area

Our puma study covered approximately 2300 km² of the southern Greater Yellowstone Ecosystem and included portions of Grand Teton National Park, the National Elk Refuge, and the Bridger-Teton National Forest. Elevations in the study area ranged from 1800 to 3600 m. The area was characterized by short, cool summers and long winters with frequent snowstorms, during which elk (*Cervus elaphus*) migrated to form large aggregations at lower elevations (18). Before the start of this research, we had estimated a conservative puma density in the study area of 0.47 resident adult pumas per 100 km² (47), which is lower than is typical in the western United States and Canada (1.5 to 1.7 resident adults per 100 km²) (48).

Puma capture, collar programming, and measuring interactions

We used trailing hounds to force pumas to retreat to a tree where we could safely capture them. Pumas were fitted with a GPS collar (Lotek Wireless Inc. models Globalstar S, Iridium M, or VECTRONIC Aerospace model GPS Plus). Our capture protocols adhered to guidelines outlined by the American Society of Mammalogists (49) and were reviewed by an independent Institutional Animal Care and Use Committee (www.iacuc.org). Further details about capture protocols and study area are found in the study by Elbroch *et al.* (18).

We programmed GPS collars to acquire simultaneous location data every 2 hours (12 times per day). GPS data were uploaded to Globalstar satellites six times per day or once per day to Iridium satellites. Upon retrieval, we identified aggregated GPS points in which ≥ 2 locations spanning ≥ 4 hours of time were within 150 m of each other. We systematically searched aggregated locations to locate and identify prey remains. 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) to record 60-s videos of activity, with a 30-s delay between videos.

We determined when two pumas were at a food resource at the same time through location data gathered by GPS collars at carcasses verified through field investigations and with video data collected by

motion-triggered cameras (24). We defined the first puma recorded on site, determined with GPS data or camera data, as the puma that made the kill and any subsequent puma that joined them as the recipient of tolerance.

Genetic methods to determine relatedness

Blood and tissue samples were collected during puma captures, from which DNA was extracted. Twenty-one cougar-specific microsatellite loci were amplified and analyzed using primers developed by Kurushima *et al.* (50). Detailed laboratory methods are described in the study by Elbroch *et al.* (51). Relatedness was described on a scale of 0 to 1: 0, completely unrelated individuals; 0.25, a typical half-sibling relation; 0.5, a typical parent-offspring relation; and 1, an individual's complete relatedness to itself.

Home-range calculations and spatial overlap

We calculated winter (1 December to 31 May) 95% fixed-kernel home ranges for pumas included in our network analysis, because winter was the season in which pumas interacted most frequently (24). We quantified kernel density estimates (KDEs) (52) and isopleths in the Geospatial Modelling Environment (53) with the smoothing factor (h) determined using the plug-in method (54). Home-range overlap (in square kilometers) between individual pumas was determined with the overlay tool in ArcGIS. We defined "spatial overlap" for our analyses as the fractional representation of puma A's KDE (the puma that made the kill and exhibited tolerance) shared by puma B's KDE (the puma receiving tolerance).

Network analyses

A directed network was constructed from instances of tolerance at food sources, which we defined as cases in which a puma killed a prey and was later joined by a second puma at the carcass. Edges in the network were directional, from the puma that killed prey and then exhibited tolerance to the puma that was tolerated at the food resource. The network also included multiple edges between two nodes, meaning that if a puma tolerated the same conspecific repeatedly, then those multiple interactions were represented. Two adult female pumas (UncF1 and UncF2) in the network were not captured or sampled. For correlation analysis and ERGMs, individual attributes, such as age, weight, relatedness, and spatial overlap, were imputed as the mean value for sampled females.

We used CUG tests (28) to determine whether network structures, including community structures (55), were found more often than would be expected by chance; in this analysis, we dichotomized edges (that is, puma A either tolerated puma B or did not), and multiple instances of tolerance were not considered. We created a null distribution of networks by simulating 10,000 networks of the same size and density as the observed network and reported the proportion of network simulations with greater network statistics of interest as P values (28, 56). Thus, the P value represented the probability of observing a greater value for a particular variable in the absence of any structuring process. We tested the following variables: direct reciprocity, defined as the fraction of edges that included puma A tolerating puma B and vice versa; hierarchical reciprocity (transitivity), the fraction of links that included the combination puma A tolerates puma B, puma B tolerates puma C, and puma A tolerates puma C; modularity, as tested via random walk permutations (57), to quantify the extent to which the network was composed of distinct communities (also called "clusters"), within which many edges occurred and between which few edges occurred; clustering, defined as the proportion of connected puma dyads that also shared edges with a third

(all shares in any direction); and in- and out-degree centralization, defined as the concentration of edges on a small number of pumas.

We also used ERGMs (25) to better tease apart the effects of partially correlated predictors and to offer additional insights into what variables explained puma tolerance. In ERGMs, edges are predicted as a function of local network structures, such as the number of edges with other pumas that two individuals share, and individual attributes, such as puma sex or weight. We estimated ERGMs for the network with both dichotomized edges and edges that represented multiple counts of tolerance between a puma dyad to account for assumptions of multiple interactions in theories of the development of social behaviors (7). For the binary network, predictor values were analogous to logistic regression coefficients. For the count-edge network, we modeled edges as a Poisson-distributed variable, and a zero-inflation term was included. We tested the following variables: Density provided a baseline likelihood of edges between pumas and provided an analogous term to an intercept term in a traditional statistical model. Direct reciprocity reflected the change in the likelihood that puma B tolerated puma A, given that puma A tolerated B. Relatedness tested for increased or decreased likelihood of puma tolerance with changing genetic relatedness shared between pumas. Spatial overlap tested for the effect of spatial overlap between pumas influencing the likelihood of puma A tolerating puma B; overlap was defined as the fractional representation of puma A's 95% KDE shared by puma B's 95% KDE. Male receiving and male sharing reflected the likelihood of tolerance exhibited to and by male pumas, respectively (versus female pumas as the base case). Hierarchical reciprocity (transitivity) tested for two pumas mutually tolerating a third puma being more likely to tolerate each other, reflecting hierarchical community structure (26). Generalized reciprocity (cyclicality) tested for triads wherein each puma both tolerated and was tolerated by one other puma, reflecting an egalitarian community effect. In our binary ERGM model, even-distribution sharing and receiving terms (geometrically weighted out- and in-degree, respectively) described the dispersal of edges; positive coefficients indicated a tendency for pumas to tolerate others in equal proportions (58). Finally, any shares in our count-edge model reflected zero-inflation; a negative value for any shares would indicate a tendency for puma dyads to have zero shares (connections) more often than expected based on the Poisson expectation.

Additional ERGM model parameters are as follows: Even-distribution terms were geometrically weighted degree terms with a decay parameter fixed to 0.5. Hierarchical and generalized reciprocity were geometrically weighted in the binary ERGM with decay parameter values fixed to 0.25. In the Poisson-distributed model, mutuality took the geometric form, and both triadic terms used the geometric mean for the two-path and affect and the sum of the paths for combination.

We constructed goodness-of-fit (GOF) plots to evaluate whether networks simulated from the ERGMs were similar to the empirical network, demonstrating that the models were well fit to the data; GOF plots are included in fig. S1. All analyses were carried out in R version 3.3.1 (59). Network analyses used the statnet suite of R packages (25, 60), except modularity, which was measured using the igraph package (61).

Testing for the effects of kinship and pair type on aggression between cofeeding pumas

We used video data to quantify aggression between adult pumas feeding together. We quantified the initial interaction between two pumas using a five-point system. Each adult was scored individually, and then, the interaction was defined as the sum of the interacting pair (range, 0 to

10 points). Our categories were meant to represent the typical aggression progression we observed in videos: 0 (least aggressive), no detectable agitation or aggression; 1, ears back and sometimes some light rumbling (growling with mouth closed); 2, short hiss and likely some low rumbling; 3, loud and long hiss and some low rumbling and louder growling with mouth open; 4, a defensive swat without contact, typically with a loud growl, or an offensive charge without contact; and 5 (most aggressive), aggressive physical contact.

We used generalized linear models (SAS 9.3, SAS Institute) with Poisson distributions to fit our selection parameter (aggression) to two sets of independent covariates: (i) We first tested whether males and females exhibited similar aggression (individual puma was included in the model as a random effect), and (ii) for those interactions for which we had genetic samples for both pumas, we tested whether aggression was explained by relatedness or pair type (male-female or female-female); the unique pair of interacting pumas was included in the model as a random effect.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/10/e1701218/DC1>

fig. S1. GOF plots.

movie S1. A typical female-female interaction at a carcass.

movie S2. A highly aggressive female-female interaction at a carcass.

movie S3. A typical male-female interaction at a carcass of prey killed by the female (F51).

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