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Table scraps: inter-trophic food provisioning by pumas

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Large carnivores perform keystone ecological functions through direct predation, or indirectly, through food subsidies to scavengers or trophic cascades driven by their influence on the distributions of their prey. Pumas (*Puma concolor*) are an elusive, cryptic species difficult to study and little is known about their inter-trophic-level interactions in natural communities. Using new GPS technology, we discovered that pumas in Patagonia provided 232 ± 31 kg of edible meat/month/100 km^2 to near-threatened Andean condors (*Vultur gryphus*) and other members of a diverse scavenger community. This is up to 3.1 times the contributions by wolves (*Canis lupus*) to communities in Yellowstone National Park, USA, and highlights the keystone role large, solitary felids play in natural systems. These findings are more pertinent than ever, for managers increasingly advocate controlling pumas and other large felids to bolster prey populations and mitigate concerns over human and livestock safety, without a full understanding of the potential ecological consequences of their actions.

Keywords: Andean condor; inter-trophic food provisioning; keystone species; Patagonia; *Puma concolor*

1. INTRODUCTION

Large carnivores perform keystone ecological functions through direct predation, as well as indirectly, by contributing food to scavenger and decomposer communities [1] and/or through trophic cascades driven by their influence on the distributions of their prey [2,3]. Yet, because of our perceived *negative* impacts of carnivores on natural and agricultural systems, numerous carnivores are threatened with extinction [4,5]. Researchers, however, are increasingly demonstrating positive and essential ecological roles performed by large carnivores in structuring and diversifying communities [6–8]. For example, grey wolves (*Canis lupus*) in North America influence such diverse ecological dynamics as aspen (*Populus tremuloides*) recruitment and songbird diversity through changing elk (*Cervus elaphus*) distributions on the landscape [2]. Wolves also subsidize sympatric scavengers, and based upon the annual contributions estimated for three years in Yellowstone National Park (YNP), provide 84.5–155.9 kg meat/month/100 km^2 to their larger ecological communities [1].

In contrast, little is known about the inter-trophic-level interactions of large, solitary felids like pumas (*Puma concolor*) [9], even while managers increasingly advocate controlling pumas and other large felids to bolster populations of endangered and declining prey species, and to alleviate ongoing concerns over human and livestock safety [10,11]. Pumas are generalist hunters of large ungulates and diverse small prey [9]. They often conceal large prey and return to the carcass multiple times to feed. On occasion, however, pumas are forced to relinquish their kills to competitors before they have finished feeding, or they may abandon their kills for other reasons. We used GPS technology to track pumas in Chilean Patagonia, find their kills and to estimate puma inter-trophic energetic contributions to other species in terms of kilograms of meat when pumas abandon their kills.

2. MATERIAL AND METHODS

Our study was conducted in Chile's Aysén District in central Patagonia (−47.12000° W, −72.2300° S; figure 1). We used hounds to force pumas to retreat to defensive habitat (either a tree or rocky outcrop) where we could safely approach and anaesthetize them. Between March 2008 and September 2009, 11 pumas were captured, nine of which were fitted with Argos-GPS collars [12]. GPS collars acquired locations at 2 h intervals and transmitted data through an Argos uplink every 2–5 days. Upon data retrieval, distances between locations were calculated in ArcGIS v. 9.1. We defined GPS clusters [13] as any more than or equal to two locations within 150 m of each other, and certified observers [14] conducted field investigations of any cluster where at minimum one location was made during the night. Field investigation occurred within 11 ± 12 days of the date the puma made the kill. Prey remains were used to identify prey and the state of remains were used to determine whether the puma had killed the animal or was scavenging.

Prey weights were estimated in kilograms from age-specific weights found in the literature [12], and we assumed that 68 per cent of an ungulate's weight [1] and 95 per cent of any small vertebrate prey [15] were edible material. Lacking actual consumption rates, we estimated the weight of meat eaten by individual pumas from the number of 24 h periods they spent at a carcass and consumption rates determined for captive pumas [16]. We used an initial consumption rate of 6.8 kg for the first 24 h and then 4.1 kg for each successive 24 h period.

The numbers of kittens for collared females were determined through captures, direct observations, by tracks in snow and/or remote cameras at kill sites. For females with kittens more than three months of age, we also estimated the amount eaten by individual kittens as the fractional proportion of their weight of an adult female's weight in the study area (34 kg) multiplied by the adult consumption rates reported above. Monthly weights of kittens were calculated from equations developed by Maehr & Moore [17] and the equation constants suggested in Laundré & Hernández [18]. Kitten consumption rates were combined with that of their mother to estimate total feeding of family groups [19].

We subtracted consumption estimates from our estimates of available edible meat at each carcass to determine the amount of meat each puma abandoned to other animals at each kill. We quantified kill rates for (animals killed per week) and the amount of meat abandoned by individual pumas we were able to monitor continuously for more than or equal to four weeks [20]. For pumas in which there was a gap in monitoring, and thus two periods of continuous monitoring more than or equal to four weeks, we calculated kill rates and amount of meat abandoned for each period separately. Given the variable number of observations across pumas, we used a mixed model Analysis of Variance (ANOVA) and a least-squares function to test whether there were differences in both kill rates and the amount of meat abandoned by males versus females (SAS v. 9.3).

Vertebrate scavengers at puma kills were documented through sightings by researchers, remote cameras and/or associated signs (e.g. droppings and footprints).

3. RESULTS

We visited 694 GPS clusters and documented 433 sites with prey remains (350 ungulates and 83 smaller vertebrates) and an additional six sites where pumas

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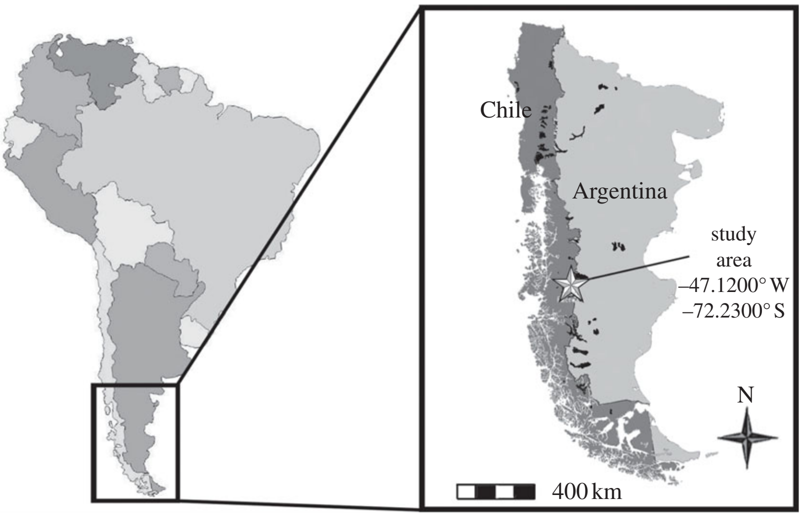

Figure 1. Study area.

Table 1. Kilograms of meat abandoned by individual pumas.

puma ID	gender	days monitored	kills made	puma ID	daily kilograms abandoned	monthly kilograms abandoned
M2	male	45	7	292	6	195
M2	male	50	6	367	7	220
M3	male	120	34	927	8	232
M3	male	164	40	1066	6	195
M4	male	79	10	314	4	119
F1[a]	female	202	38	1135	6	169
F2[b]	female	62	10	317	5	154
F3[c]	female	169	50	1647	10	292
F4[d]	female	421	110	1568	4	112
F5[e]	female	208	53	223	1	32

[a]Two 3-months kittens at capture.
[b]Zero kittens for duration of monitoring.
[c]Two 6-months kittens at capture, one died after 58 days of monitoring.
[d]Two kittens born after 202 days of monitoring.
[e]Three kittens born on day 139 of monitoring

were scavenging already dead prey [12]. Excluding the scavenging data, we quantified kill rates for eight pumas (three males and five females) with sufficient Argos data transmissions for continuous monitoring (table 1). On average, individual pumas in our Patagonian study killed 6.5 ± 1.8 animals per month, and abandoned 171.9 ± 72.8 kg of edible meat to scavengers and decomposers. Both kill rates (mixed-model ANOVA: $F_{1,4.74} = 0.85$, $p > 0.4019$) and the amount of meat abandoned (mixed-model ANOVA: $F_{1,5.82} = 0.23$, $p > 0.6466$) by males and females were equivalent (table 1). Based upon our density estimates of 1.35 resident adult pumas per 100 km^2 [12], pumas made inter-trophic contributions of $232.1 \pm$ s.e. 31.1 kg meat/month/100 km^2, and 2553 kg meat/month over our 1100 km^2 study area.

We documented Andean condors (*Vultur gryphus*; figure 2*a*) at 43 per cent ($n = 126$) of ungulates killed by pumas in which we could confidently determine whether condors were present or not, and 11 additional vertebrate scavengers: black vulture (*Coragyps atratus*), culpeo fox (*Lycalopex culpaeus*; figure 2*b*), Patagonia hog-nosed skunk (*Conepatus humboldti*), southern caracara (*Caracara plancus*), chimango caracara (*Milvago chimango*), white-throated caracara (*Phalcoboenus albogularis*), black-chested buzzard eagle (*Geranoaetus melanoleucus*), great shrike tyrant (*Agriornis livida*), Austral blackbird (*Curaeus curaeus*), thorn-tailed rayadito (*Aphrastura spinicauda*) and a lizard (*Liolaemus* sp).

4. DISCUSSION

Based upon consumption rates of captive pumas, we estimated that pumas in Patagonia contributed up to 3.1 times more food to their ecological communities than wolves in YNP [1]. This is probably a conservative estimate because our puma density estimates did not include transient pumas, which were also abandoning meat at their kills. In addition, pumas are found at lower densities than wolves (3.44 pumas/100 km^2 in our study, including known kittens [12] versus 4.8–10.6 wolves/100 km^2 in YNP [21]). Therefore, food provisioning by individual pumas is even larger than contributions made by individual wolves than these data suggest. This disproportion is in part due to the solitary nature of pumas. Kaczensky *et al.* [22] showed that the size of a wolf pack influences foraging success by competitive scavengers, and that larger packs more efficiently consumed carcasses before scavengers;

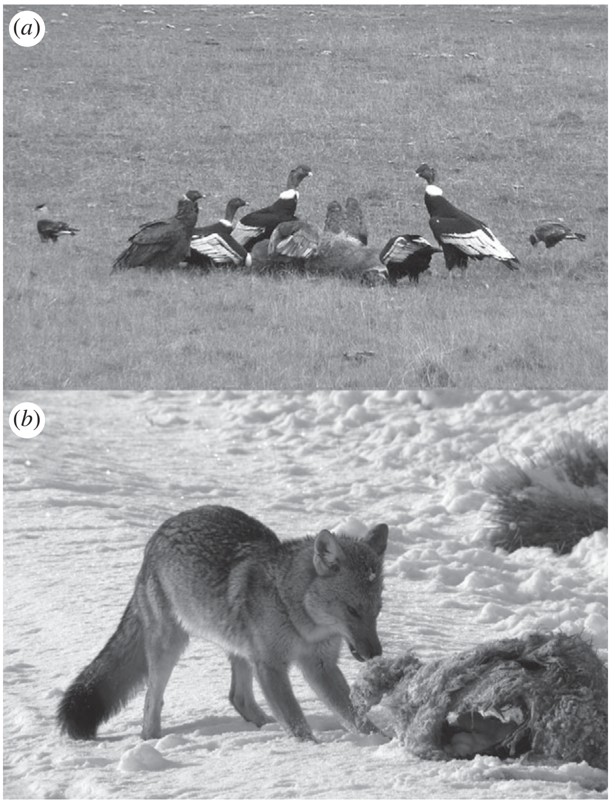

Figure 2. (*a*) Large Andean condors and a pair of smaller southern caracaras surround a guanaco (*Lama guanicoe*) killed by a female puma in Patagonia. (*b*) A culpeo fox scavenging from a guanaco carcass abandoned by a female puma.

wolves also defend their kills from competitors [21]. Solitary felids, by contrast, often retreat to cover to remain unobtrusive and minimize conflicts with other competitors [23], and thus are more susceptible to kleptoparatism.

Our findings suggest that managers need to weigh the benefits of puma culling with the potential negative ecological impacts of puma removal. Here, we reveal that the direct effects of pumas on community assemblages include more than just predation, and include numerous positive effects as well. Pumas suffer continued persecution because of perceived threats to humans and livestock, and are increasingly controlled to aid rare species recovery [10,11]. Food provided by pumas may be vital to the maintenance and diversity of scavenger and decomposer communities in Patagonia and elsewhere. We documented 12 vertebrate scavengers at puma kills (figure 2), including the iconic, IUCN near-threatened Andean condor [24], a carrion-dependent species that we documented at 43 per cent of ungulate kills. Our research offers a critical first step in understanding the keystone ecological roles of large, solitary felids in natural systems, and more generally, should be considered in future management and conservation strategies for all large felids.

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