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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 due to 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 km² 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 of solitary felids 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 km² to their larger ecological communities [1].
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 ± 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 2a) 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 2b), Patagonia hog-nosed skunk (Conepatus humboldti), southern caracara (Caracara plancius), 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).

### Table 1. Kilograms of meat abandoned by individual pumas.

<table>
<thead>
<tr>
<th>Puma ID</th>
<th>Gender</th>
<th>Days Monitored</th>
<th>Kills Made</th>
<th>Puma ID</th>
<th>Daily Kilograms Abandoned</th>
<th>Monthly Kilograms Abandoned</th>
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<tr>
<td>M2</td>
<td>Male</td>
<td>45</td>
<td>7</td>
<td>M2</td>
<td>6</td>
<td>292</td>
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<td>6</td>
<td>M2</td>
<td>7</td>
<td>367</td>
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<tr>
<td>M3</td>
<td>Male</td>
<td>120</td>
<td>34</td>
<td>M3</td>
<td>8</td>
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<td>Male</td>
<td>164</td>
<td>40</td>
<td>M3</td>
<td>6</td>
<td>1066</td>
</tr>
<tr>
<td>M4</td>
<td>Male</td>
<td>79</td>
<td>10</td>
<td>M4</td>
<td>4</td>
<td>314</td>
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<tr>
<td>F1$^a$</td>
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<td>202</td>
<td>38</td>
<td>F1$^a$</td>
<td>6</td>
<td>1155</td>
</tr>
<tr>
<td>F2$^b$</td>
<td>Female</td>
<td>62</td>
<td>10</td>
<td>F2$^b$</td>
<td>5</td>
<td>317</td>
</tr>
<tr>
<td>F3$^c$</td>
<td>Female</td>
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<td>50</td>
<td>F3$^c$</td>
<td>10</td>
<td>1647</td>
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<td>110</td>
<td>F4$^d$</td>
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<td>Female</td>
<td>208</td>
<td>53</td>
<td>F5$^e$</td>
<td>1</td>
<td>223</td>
</tr>
</tbody>
</table>

$^a$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.

### 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 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;
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 kleptoparasitism.

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 to aid rare species recovery [10,11]. Food provided humans and livestock, and are increasingly controlled to aid rare species recovery [10,11]. Food provided

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.

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