NOTES AND COMMENTS

Scavenging by fishers in relation to season and other scavengers

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Abstract
Carrion is an energy-rich resource that benefits many organisms, but scavenging involves both profits and risks. Fishers (Pekania pennanti) are forest-specialists that scavenge large carcasses but quantitative assessments of their scavenging are lacking. We quantified three characteristics of scavenging behavior by fishers: (a) whether fishers visited a carcass; (b) the time to first visitation of a carcass by fishers; and (c) how long fishers fed at a carcass. We then evaluated the importance of habitat characteristics, cues from other scavenger species, and season on the scavenging behaviors of fishers. Fishers scavenged 25 of the 89 deer carcasses we monitored, and visited carcasses more frequently in winter (n = 22, 34%) than in summer (n = 3, 12%). Time to the first fisher visit to a carcass averaged 4.7 (±1.1 SE) days. On average fishers made 26 (±9 SE) repeat visits to each carcass they found and fed for 118.1 min (±42.3 SE) over an average of 6 days; season also influenced their feeding times (120.3 ± 46.0 SE min in winter versus 63.7 ± 44.7 SE min in summer). Fishers had a crepuscular activity pattern while scavenging, but initial visits peaked mid-day in addition to a peak near sunset. Our results suggested that fishers may use cues from other scavengers to detect carrion, but that habitat characteristics did not affect exploitation of carrion more than other variables. These results highlight the potential importance of carrion for the foraging ecology of fishers, particularly during times of resource scarcity. Further research based on identifiable individuals is needed to quantify fitness consequences of scavenging for fishers, including possible negative effects of intraguild predation at carrion.

KEYWORDS
carrion, detection, fisher, Pekania pennanti, scavenging

1 | INTRODUCTION

Carrion, especially large carcasses, is a nutritious and inexpensive resource that benefits many organisms (Inagaki et al., 2020; Sebastián-González et al., 2020). Carrion may be more important for animals experiencing resource scarcity (Barrio, Hik, Bueno, & Cahill, 2013; O’Malley, Elbroch, Lendrum, & Quigley, 2018; Prugh & Sivy, 2020), but visiting carcasses also poses risks, especially for smaller vertebrate scavengers that may be injured or killed by larger scavengers or the carnivores that killed the prey. These risks can be species-specific, and how individuals of a species respond to risk can determine how frequently they scavenge and how much...
nutrition they gain from carrion (Allen, Elbroch, Wilmers, & Wittmer, 2015; Sivy, Pozzanghera, Grace, & Prugh, 2014).

Fishers (Pekania pennanti) are semi-arboreal mustelids that are of conservation concern in the Pacific US states of Washington (listed as “endangered” by the Washington Fish and Wildlife Commission), Oregon (listed as “sensitive in the critical category” by the Oregon Fish and Wildlife Office), and California (listed as “endangered” in the Southern Sierra Nevada by the U.S. Fish and Wildlife Service). They are forest-specialists of northern habitats in North America (Powell, 1993) extending into mid-elevations in the southern Sierra Nevada in California (Green, Purcell, Thompson, Kelt, & Wittmer, 2018; Powell, 1993). Fishers are generalist carnivores that prey mostly on lagomorphs and tree squirrels, as well as porcupines (Erethizon dorsatum) and other small prey. They are also one of many mesocarnivores that scavenge from large animal carcasses (e.g., ungulates and bears; Hüner & Peter, 2013; Powell, 1993). Scavenging may be an important nutritional component of fisher diet, as they often stay near carcasses for multiple days (Powell, 1993) and female fishers sometimes choose den sites near large carcasses (Powell & Zielinski, 1994). Nonetheless, qualitative and quantitative descriptions of their scavenging behaviors, including habitat specific detection probabilities, feeding behavior, and seasonal importance, are lacking.

Here, we report on the scavenging behaviors of fishers at the southern limit of their range in coastal California. We analyzed four primary variables: (a) whether fishers detected each carcass we placed in different habitats; (b) how long the first fisher took to detect a carcass; (c) the total duration fishers fed at each carcass; and (d) the temporal patterns of fishers scavenging, comparing the time of day when fishers initially visited carcasses to the time of day for subsequent visits. We then evaluated the importance of habitat characteristics (Elbroch, Lendrum, Allen, & Wittmer, 2015), presence of other scavengers (Sebastián-González et al., 2020), and season (O’Malley et al., 2018) on the scavenging behaviors of fishers.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted our study across approximately 1,000 km² of the Mendocino National Forest, California (Figure 1), ranging in elevation from approximately 400 to 2,450 m. The area is primarily forested (main forest habitats include mixed hardwood conifer, Klamath mixed conifer, Douglas fir, montane hardwood, and ponderosa pine stands) with intermixed scrub and annual grasslands, that vary based on elevation. Mean daily temperatures ranged from −1°C to 24°C with mean annual precipitation averaging 132 cm (Allen, Elbroch, Casady, & Wittmer, 2015). Precipitation primarily fell during the wet winter season (November to May), with only trace

![Fisher Present](image1)

![Fisher Present](image2)

**FIGURE 1** The location of deer carcasses scavenged by fishers during our study, conducted in the Mendocino National Forest and surrounding lands in northern California [Color figure can be viewed at wileyonlinelibrary.com]
precipitation in the dry summer season (June to October). Black-tailed deer (*Odocoileus hemionus columbianus*) were the most common ungulates in the study area, along with low densities of other ungulates: wild pigs (*Sus scrofa*), tule elk (*Cervus canadensis nannodes*), and domestic cattle (*Bos taurus*) (Allen, Elbroch, Casady, & Wittmer, 2015). Common scavengers documented at mountain lion (*Puma concolor*) kills in the study area included American black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), and turkey vultures (*Cathartes aura*; Allen, Elbroch, Wilmers, & Wittmer, 2015). Known predators of fishers found in the study area included mountain lion, bobcat, coyote and domestic dogs (*Canis lupus familiaris*; Gabriel et al., 2015).

### 2.2 Field methods

We deployed video camera traps with infrared flash (Cuddeback IR, De Pere, WI) at 100 black-tailed deer carcasses to document scavenger activity and feeding behavior from December 2009–October 2012. We collected fresh carcasses of black-tailed deer killed by vehicle collisions on highways in Mendocino, Lake, Glenn, Sonoma, and Marin Counties. All carcasses were in good condition with clear, unclouded eyes, no discoloration in the abdominal region, and no obvious wounds. Because we removed heads, entrails, and lungs prior to transporting carcasses, as required by the California Department of Fish and Wildlife to limit disease transmission among deer populations, small scavengers did not depend on large scavengers to open carcasses for them. We anchored each carcass in place with a cable attached to a tree. We placed a camera trap nearby and programmed it to record the maximum amount of activity (30 s of video with a pause of 60 s before the next trigger). We excluded data from camera traps where the camera trap or carcass were displaced by black bears or the camera otherwise malfunctioned (*n* = 11).

We placed carcasses in a stratified manner to sample diverse microhabitat covariates and to ensure that sampling was representative of the local, vertebrate, scavenger guild. We focused on placing at least 10 carcasses in each of the main forested habitats found in the study area with a mix of elevation and canopy cover. At each site, we documented elevation using a handheld GPS, measured the slope of the immediate area using a clinometer, and measured the canopy cover directly above the carcass using a spherical convex densitometer. We obtained the temperature from weather station data (NOAA-Mendocino Pass, CA Weather Station; http://www.ncdc.noaa.gov/cdo-web/), using the temperature on the day, we placed the carcass as the covariate. We also included other scavenger species that were present at ≥25% of the carcasses where fishers scavenged as covariates that might affect scavenging behavior of fishers (*n* = 12, *n* = 12, *n* = 12, *n* = 6).

### 2.3 Statistical analyses

We used program R version 3.6.2 (R Core Team, 2019) for all of our statistical analyses. We tested a series of covariates using generalized linear models for three dependent variables: (a) whether fishers detected a carcass using a binomial link; (b) how long it took fishers to detect carcasses using a gamma link; and (c) the total feeding time of fishers using a Gaussian link. We were unable to conclusively determine the identity or sex of fishers, and so we assessed visitation rates at the species level. We used *z*-scores to standardize all continuous covariates prior to analyses, and then estimated effect sizes directly from estimated standardized model coefficients (Fieberg & Johnson, 2015). We used an AIC framework, using a balanced model design where we analyzed each variable and combinations of each pair of variables (Symonds & Moussalli, 2011). We selected our top models based on the AICc values, considering models with Δ1 < 2 to be our top models (Burnham & Anderson, 2002). We selected the top variables using their model averaged weight and compared their effects based on their standardized coefficients (Symonds & Moussalli, 2011).

We used kernel density estimation to determine activity patterns and quantify overlap between when fishers initially discovered carcasses versus all subsequent visits (Ridout & Linkie, 2009). We used the time each visit started as our time values in the analyses and changed the time of each event to radians that corresponded to sun time. We then used the *overlap* package (Meredith & Ridout, 2017) to fit the data to a circular kernel density and estimated the activity among time periods from the distribution of the kernel density using Δ1 (based on our sample sizes). We used the *overlapEst* function to estimate the degree of overlap in activity between when fishers initially discovered carcasses versus all subsequent visits.

### 3 RESULTS

Fishers scavenged 25 of the 89 deer carcasses we monitored (28%) and on average made 26 (±8.97 SE) visits to
each carcass. Fishers visited carcasses significantly more often in winter (34%) than summer (12%; \( z = 2.11, p = .03 \); Figure 2). Considering data from all 89 carcasses, fishers were the fifth most frequent scavenger we detected after black bears (\( n = 49 \)), gray foxes (\( n = 38 \)), turkey vultures (\( n = 30 \)), and coyotes (\( n = 29 \)). We obtained six top models for detection (Table 1, Table S1), with the top two models being the number of scavengers + temperature (\( w = 0.18 \)) and the number of scavengers + season (\( w = 0.14 \)). The top variable across all models was number of scavengers (\( \sum w = 0.87, \beta = 0.49 \)), which was nearly four times more likely to appear in a top model for fishers detection of carcasses than the next best variable (temperature; Table 2).

![FIGURE 2](wileyonlinelibrary.com)  
**FIGURE 2** The monthly values for deer carcasses detected by fishers and the mean total feeding time by fishers at carcasses [Color figure can be viewed at wileyonlinelibrary.com]

**TABLE 1** Top models for fishers detection, time to detect carcasses, and total feeding time at carcasses. We report the variables along with their AICc, difference in AICc from the top model (\( \Delta \)), AICc weight (\( w \)), and coefficients with standard error (\( \beta \pm SE \))

<table>
<thead>
<tr>
<th>(a) Detection</th>
<th>Variable</th>
<th>AIC</th>
<th>( \Delta \text{AIC} )</th>
<th>( w )</th>
<th>( \beta \pm SE )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of scavengers + temperature</td>
<td>97.05</td>
<td>0.00</td>
<td>0.18</td>
<td>0.46 ± 0.16, −0.08 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>Number of scavengers + season</td>
<td>97.52</td>
<td>0.47</td>
<td>0.14</td>
<td>0.45 ± 0.16, 1.08 ± 0.70</td>
</tr>
<tr>
<td></td>
<td>Number of scavengers + bear</td>
<td>97.53</td>
<td>0.48</td>
<td>0.14</td>
<td>0.53 ± 0.16, −0.86 ± 0.53</td>
</tr>
<tr>
<td></td>
<td>Number of scavengers + canopy cover</td>
<td>97.70</td>
<td>0.64</td>
<td>0.13</td>
<td>0.46 ± 0.16, 2.35 ± 2.17</td>
</tr>
<tr>
<td></td>
<td>Number of scavengers + elevation</td>
<td>97.77</td>
<td>0.72</td>
<td>0.12</td>
<td>0.51 ± 0.16, 0.01 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>Number of scavengers</td>
<td>98.12</td>
<td>1.06</td>
<td>0.10</td>
<td>0.49 ± 0.15</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(b) Detection time</th>
<th>Variable</th>
<th>AIC</th>
<th>( \Delta \text{AIC} )</th>
<th>( w )</th>
<th>( \beta \pm SE )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coyote</td>
<td>133.17</td>
<td>0.00</td>
<td>0.10</td>
<td>2.94 ± 1.93</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>133.50</td>
<td>0.34</td>
<td>0.08</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Season + coyote</td>
<td>134.21</td>
<td>1.05</td>
<td>0.06</td>
<td>−3.21 ± 3.63, 3.43 ± 1.86</td>
</tr>
<tr>
<td></td>
<td>Number of scavengers</td>
<td>134.30</td>
<td>1.13</td>
<td>0.06</td>
<td>0.79 ± 0.64</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>134.62</td>
<td>1.46</td>
<td>0.05</td>
<td>0.22 ± 0.17</td>
</tr>
<tr>
<td></td>
<td>Coyote + gray fox</td>
<td>134.70</td>
<td>1.53</td>
<td>0.05</td>
<td>2.87 ± 1.68, 1.69 ± 1.49</td>
</tr>
<tr>
<td></td>
<td>Gray fox</td>
<td>135.06</td>
<td>1.90</td>
<td>0.04</td>
<td>1.80 ± 2.02</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(c) Total feeding time</th>
<th>Variable</th>
<th>AIC</th>
<th>( \Delta \text{AIC} )</th>
<th>( w )</th>
<th>( \beta \pm SE )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Null</td>
<td>340.35</td>
<td>0.00</td>
<td>0.07</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>341.25</td>
<td>0.90</td>
<td>0.05</td>
<td>6.62 ± 5.22</td>
</tr>
<tr>
<td></td>
<td>Gray fox</td>
<td>341.57</td>
<td>1.22</td>
<td>0.04</td>
<td>92.59 ± 81.11</td>
</tr>
<tr>
<td></td>
<td>Black bear</td>
<td>341.65</td>
<td>1.29</td>
<td>0.04</td>
<td>−90.70 ± 81.76</td>
</tr>
<tr>
<td></td>
<td>Coyote</td>
<td>341.81</td>
<td>1.46</td>
<td>0.04</td>
<td>84.42 ± 81.50</td>
</tr>
<tr>
<td></td>
<td>Bobcat</td>
<td>341.85</td>
<td>1.50</td>
<td>0.03</td>
<td>−96.96 ± 95.42</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>341.88</td>
<td>1.53</td>
<td>0.03</td>
<td>−9.97 ± 9.98</td>
</tr>
<tr>
<td></td>
<td>Canopy cover</td>
<td>342.00</td>
<td>1.64</td>
<td>0.03</td>
<td>393.60 ± 416.51</td>
</tr>
<tr>
<td></td>
<td>Gray fox + slope</td>
<td>342.03</td>
<td>1.68</td>
<td>0.03</td>
<td>110.56 ± 79.96, 7.70 ± 5.17</td>
</tr>
<tr>
<td></td>
<td>Coyote + gray fox</td>
<td>342.13</td>
<td>1.78</td>
<td>0.03</td>
<td>120.09 ± 82.57, 126.46 ± 82.56</td>
</tr>
<tr>
<td></td>
<td>Elevation</td>
<td>342.32</td>
<td>1.97</td>
<td>0.03</td>
<td>0.23 ± 0.30</td>
</tr>
</tbody>
</table>
Fishers on average took 4.7 (±1.1 SE) days to detect carcasses. The top models for detection time were equivalent and included the null model (Table 1). The top variable explaining detection time across all models was the presence of coyotes (\( p = 0.31, \beta = 2.9 \), Table 2).

Fishers on average fed for 118.1 min (±42.3 SE) at each carcass they found and spent an average of 5.7 min (±0.9 SE) during each visit. None of the covariates that we tested to explain variation in total feeding time improved model fit over the null model (Table 1). There was no relationship between the time to detect a carcass and total feeding time (\( R^2 = -0.04, p = .97 \)), but fishers scavenged for longer in winter (\( 120.3 \pm 46.0 \) SE min) than in summer (\( 63.7 \pm 44.7 \) SE min; Figure 2). Top model averaged variables included slope (\( \sum \omega = 0.21, \beta = 6.6 \)), presence of gray foxes (\( \sum \omega = 0.19, \beta = 92.6 \)), and presence of bobcats (\( \sum \omega = 0.17, \beta = -97.0 \)) (Table 2), but these variables did not perform better than the null model when modeled individually.

Fishers scavenged throughout the day and night (Figure 3). The time of day when fishers initially discovered carcasses overlapped strongly with all subsequent visits (\( \Delta_1 = 0.86 \), but initial visits had a peak mid-day along with near sunset while subsequent visits had a crepuscular pattern.

### DISCUSSION

Our results highlight the importance of scavenging in the foraging ecology of fishers, particularly during times of resource scarcity and high energetic demands (i.e., Stress Gradient Hypothesis; Barrio et al., 2013). Fishers in our study scavenged from nearly as many carcasses (28%) as did turkey vultures (34%), which are key obligate scavengers in scavenger communities worldwide (Sebastián-González et al., 2020). Large carcasses can provide substantial food with no handling costs compared to the small- and medium-sized prey fishers usually kill and consume (LaPoint, Belant, & Kays, 2015). Fishers visited carcasses more frequently (34% of carcasses) and fed for twice as long in winter than in summer, as do other mesocarnivores (e.g., red fox, *Vulpes vulpes*; Selva, Jedrzejewska, Jedrzejewski, & Wajrak, 2005; O’Malley et al., 2018). Fishers exhibit delayed implantation, rapid fetal growth in the final month of pregnancy, and give birth in late winter (mean date of parturition across their range is 25 March; Green et al., 2018). Therefore scavenging may be more important when fishers are energetically stressed.

Despite monitoring a large number of carcasses, our study was limited by small effective sample sizes for...
fishers ($n = 25$). Nevertheless, we found that the number of species that scavenged carcasses was the most important variable explaining whether fishers also visited carcasses. We interpret this result to mean that fishers use cues from other scavengers to locate carcasses, similar to conclusions about how scavengers detect carrion more broadly drawn in other studies (Sebastián-González et al., 2016; Wilmers, Stahler, Crabtree, Smith, & Getz, 2003). However, the resulting overlap with other, often dominant, scavengers at carcasses may also have negative fitness consequences for fishers (i.e., the Fatal Attraction Hypothesis; Prugh & Sivy, 2020; Sivy, Pozzanghera, Grace, & Prugh, 2017). For example, pumas, bobcats, and coyotes kill fishers (Gabriel et al., 2015) and fishers in our study system were sometimes killed by pumas while scavenging from deer killed by these apex predators (Allen, Elbroch, Casady, & Wittmer, 2015; Allen, Elbroch, Wilmers, & Wittmer, 2015). The mix of positive and negative interactions at carcasses may be indicative of the complexity of interspecific interactions that can occur within vertebrate scavenging communities (Peers et al., 2020; Prugh & Sivy, 2020; Sebastián-González et al., 2020).

The Mendocino National Forest is generally thought to be the southernmost extent of the distribution of fishers in coastal areas (but see Allen, Evans, & Gunther, 2015), but little is known about this population. Our results show that fishers in this region regularly scavenge carcasses, especially in winter, but there is much we still do not know about the scavenging behavior of fishers. For example, our analyses aimed at understanding both carcass detection and feeding times were inconclusive. We were also unable to conclusively determine the sex of fishers scavenging carcasses. Due to their sexual dimorphism, sex influences energetic demands and likely influences predation risk and thus potentially their use of carrion. To clearly understand sex-specific positive and negative fitness consequences associated with the use of carrion, future research will likely require identifiable fishers marked with telemetry equipment. Given the conservation status of many western fisher populations, and the impact of large carnivores on carrion distributions and abundance, we encourage further work to better understand whether carrion resources increase intraguild predation on fishers or whether dominant competitors like pumas are in fact facilitating fisher populations in need (Prugh & Sivy, 2020).

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REFERENCES


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