SPATIAL MEMORY

Ravens anticipate wolf kill sites across broad scales

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Scavengers generally rely on patchily distributed, unpredictable carrion. A long-standing hypothesis suggests scavenging ravens reliably locate such food by directly following large carnivores to their kills. However, by satellite tracking 69 ravens, 20 wolves, and 11 cougars in Yellowstone National Park, we found that following of predators over large distances rarely occurred. Instead, ravens routinely revisited sites where wolf kills were common—returning from distances of up to 155 kilometers to find carrion. Much like navigating to permanent anthropogenic subsidies, ravens appear to remember potential sources of carrion shaped by previous encounters with wolves or their kills. These findings suggest that spatial memory and navigation play a considerably greater role than previously assumed among scavengers, and possibly other wide-ranging species, in search of ephemeral resources.

Most animals live in dynamic environments where resource availability and predictability vary in space and time. When predictability is high, many animals use spatial memory to improve foraging efficiency (*1–4*). When resources are unpredictable, animals are hypothesized to rely less on memory and more on perceptual cues, random searches, or social information exchange (*5*, *6*). Scavengers that exploit the kills of predators face the challenge of finding a food source that is relatively unpredictable in both space and time (*7*), and are often short-lived due to the presence of a large number of competitors (*8*, *9*). The availability of carrion produced by predators depends on the interaction between prey abundance and predator hunting behavior (*10*). As a consequence of this carrion provisioning, scavengers are found in proximity to or even following large carnivores, particularly species that kill prey too large for immediate consumption (*11–14*). Although numerous studies focus on scavengers' morphological, physiological, or social adaptations for finding carrion efficiently (*15*), little is known about individual movement strategies and the role of spatial memory versus direct cueing for locating kills of large carnivores.

We tested a long-standing hypothesis that scavengers adjust their movements to follow large carnivores. Although scavengers are frequently observed near large carnivores in the field—sometimes even engaging in short-distance following behavior—it remains unclear whether following behavior reflects a frequent foraging strategy over larger spatial and temporal scales. We contrast this with an alternative hypothesis, that scavengers locate carrion by proactively revisiting sites where carrion is likely to recur as a result of high carnivore abundance or kill density. This alternative implies the use of spatial memory from prior encounters with large carnivores and/or their kills, rather than relying on real-time cueing to predator locations.

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We focused on the scavenger-predator system of common ravens (*Corvus corax*) and gray wolves (*Canis lupus*), as well as the sympatric system of ravens and cougars (*Puma concolor*), another large carnivore with similar prey (*16*, *17*). Although little is known about raven-cougar interactions, ravens are the most prominent scavenger species at wolf kills in many regions (*9*, *10*). Ravens have been observed cueing on and flying with traveling wolves (*18*), following wolf tracks in the snow (*11*), orienting toward wolf howling (*19*), and aggregating rapidly at fresh wolf kills (*20*). These associations suggest that ravens directly follow wolves as a viable winter foraging strategy, when finding carrion can be most difficult yet crucially important (*20*). Scavengers that follow large carnivores are expected to reduce search effort and intraguild competition by directly observing predation or being led to recently made kills. By contrast, revisiting previously successful sites is expected to be cognitively more demanding as it requires predicting the behavior and space use of another species, indicative of the distribution of their kills. Ravens are ideal candidates for testing this idea as they are known for their advanced cognitive abilities. For example, ravens use spatial memory to retrieve food from their caches and steal those of conspecifics and heterospecifics (*21–23*). The future-planning abilities of ravens are similar to those of great apes (*24*) and show elements of theory of mind (*25*), which may aid in predicting and interpreting the behavior of other scavengers or predators. We tested whether ravens follow large carnivores, how often they co-occurred with them, how such co-occurrence translated into the use of their kills, and—if ravens were not found to follow large carnivores—whether their use of kills could instead be explained by revisiting areas of previous kills.

Multispecies tracking to study scavengers' adaptations to large carnivore movements

Over 2.5 years, we collected 646,494 locations from 69 ravens, 77,085 locations from 20 wolves (from six packs and one loner), and 58,269 locations from 11 cougars equipped with Global Positioning System (GPS) devices in Yellowstone National Park, or within 5 km of its boundaries (Fig. 1 and fig. S1). Additionally, we recorded location and date of ungulates killed by wolves (n = 355) or cougars (n = 137), based on

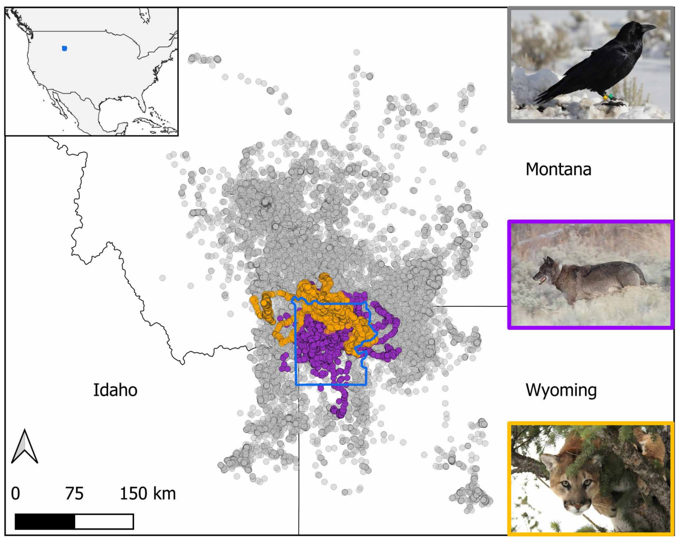

Fig. 1. Movements of GPS-tracked ravens, wolves, and cougars in MT, WY, and ID, USA. From October 2019 through March 2022, all locations of ravens (gray), wolves (purple), and cougars (orange) are shown, except for the GPS positions of two ravens after dispersing more than 350 km from all carnivores. The blue polygons in the large map and inset represent the boundaries of Yellowstone National Park and the black lines refer to state borders. Photo credit: M.-C.L.

field observations and ground-truthed GPS clusters from collared individuals (fig. S2). For carnivores, GPS-sampling frequency was highest during six monthly winter study periods, and parts of the analyses specifically focus on these months [see supplementary materials (SM)]. All large carnivores showed home-ranging or territorial behavior and remained within the core study area (Fig. 1). Ravens, space use varied by life stages: 26 were year-round territorial residents within or close to wolf territories and 43 were vagrant nonterritorial wanderers throughout the Greater Yellowstone Ecosystem. The distinction between territorial and vagrant ravens was based on central-place foraging with repeated use of the same night roosts versus nomadic movements with frequent changes of night roosts, respectively (see SM). During winter, both territorial and vagrant ravens showed, on average, higher daily displacement compared with the carnivores (fig. S3 and tables S1 to S3; see table S4 for a comparison of seasonal space use).

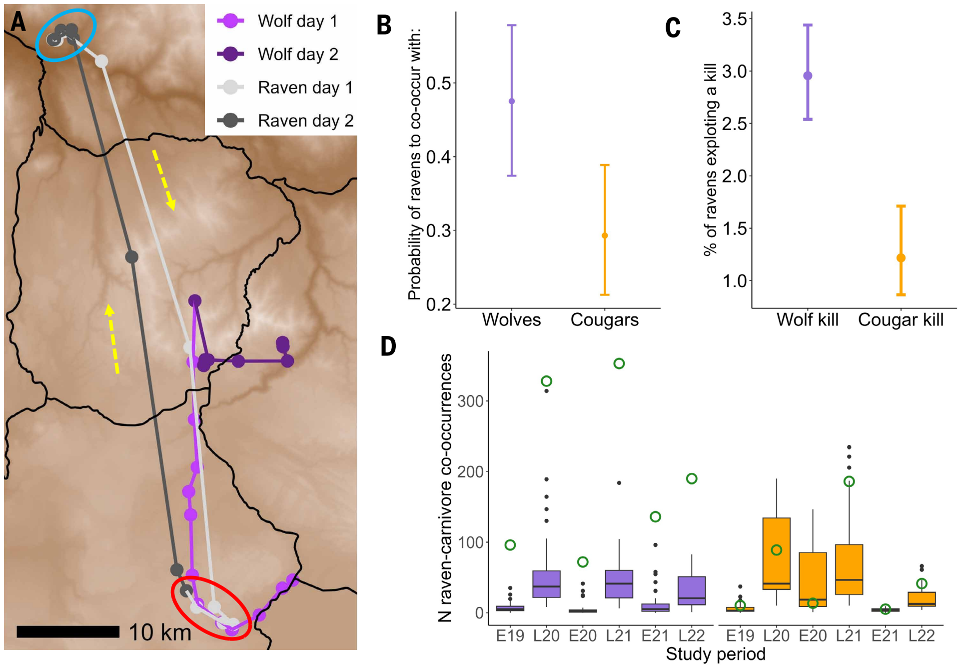

Fig. 2. Co-occurrences between ravens and large carnivores. (**A**) A vagrant raven flew directionally from an area with anthropogenic subsidies (blue ellipse) outside Yellowstone National Park, traveling ~60 km to a wolf territory (direction indicated by the yellow arrow), where it encountered a GPS-collared wolf. Raven and wolf remained in proximity, moving 4 km over 2 hours (red ellipse), representing the only instance of long-distance following recorded in 2.5 years. While the raven roosted overnight, the wolf continued moving, and the raven returned to the anthropogenic subsidies the next day. Points and colored lines represent GPS locations with interpolated movement trajectories. Black lines indicate main roads and the brown gradient shows elevation from 1500 m (dark) to 3500 m (light), illustrating that this raven was not simply following landscape features. (**B**) The probability of a raven co-occurring with a wolf was significantly higher than with a cougar. Model predictions refer to at least one co-occurrence during a 1-month winter study period. (**C**) Ravens exploited wolf kills more frequently than cougar kills. Model estimates show the percentage of all GPS-tagged ravens using wolf or cougar kills within the first 7 days postmortem. (**D**) Ravens were attracted to wolves. Green circles show the observed co-occurrences between ravens and either wolves or cougars during each 1-month winter study period. Colored boxplots represent expected co-occurrence counts under a null model generated by randomizing daily carnivore trajectories (wolves, purple; cougars, orange). Ravens co-occurred with wolves significantly more often than that expected by chance.

Individual ravens rarely followed wolves, but co-occurred with them more often than with cougars

Ravens were capable of following wolves over considerable distances and extended periods; however, this behavior was rare. Over 2.5 years of tracking, we recorded only one instance of long-distance following—defined here as co-occurrence for >1 hour while moving over a distance >1 km. In this case, a vagrant raven and a wolf moved together in the same direction for 4 km over a period of 2 hours (Fig. 2A). Although a higher GPS sampling frequency or more GPS-tagged individuals could have revealed additional observations of this behavior, following over longer distances cannot be considered a common nor successful strategy for locating wolf kills. Following must be even less likely for cougar kills, as we found no raven-cougar following events.

Both vagrant and territorial ravens were significantly more likely to co-occur at least once during a 1-month winter study period with a GPS-collared wolf than with a GPS-collared cougar [back-transformed mean probability = 0.48, 95% confidence interval (CI) = 0.38 to 0.59 for wolves; mean probability = 0.29, 95% CI = 0.21 to 0.39 for cougars; Fig. 2B; model coefficients: table S5]. Given the predominantly open landscape, we defined co-occurrence as a raven and a carnivore within 500 meters of each other (see SM). Notably, in all six winter studies, the observed number of raven-wolf co-occurrences was higher than randomly expected based on permutations of daily GPS trajectories—unlike co-occurrences with cougars (Fig. 2D). This demonstrates that ravens may have intentionally associated with wolves whereas co-occurrence with cougars likely resulted from random overlap or opportunistic use of the same resources.

Ravens' above random chance associations with wolves resulted in measurable foraging benefits. Overall, 48.5% of the wolf kills and 24.8% of the cougar kills were used by at least one GPS-tagged raven during the first 7 days postmortem. A significantly greater proportion of GPS-tagged ravens exploited ungulates killed by wolves compared with cougar kills (back-transformed mean proportion = 0.029, 95% CI = 0.025 to 0.034 for wolves; mean proportion = 0.012, 95% CI = 0.009 to 0.016 for cougars; odds ratio = 0.405, $z = -4.86$, $P < 0.0001$; Fig. 2C, table S6; and see fig. S4 and table S7 for an analysis using a binary response variable). These proportions appear low because we included all GPS-tagged ravens within 350 km of a GPS-collared carnivore—a radius slightly greater than the maximum observed return distance (327 km) to the study area. Wolf packs are relatively conspicuous during hunting, as they operate in groups, mainly in open areas (*26*), and sometimes provide acoustic cues by howling when initiating a hunt or near a kill (*27*, *28*). By contrast, cougars kill less frequently (per capita), forage alone (except for mothers with kittens), cover their kills between feedings to conceal them from scavengers, and hunt using ambush and stalking strategies, primarily in topographically rugged, forested terrain within our study area (*16*, *17*). These differences likely make wolves more detectable to scavengers such as ravens, even without consistent following behavior and regardless of whether the ravens are vagrants or territorial individuals residing within wolf territories.

Site revisits over large distances

Ravens benefited from their associations with wolves but demonstrated a more dynamic strategy than simply following individual wolves or packs. Instead of consistently remaining near carnivores, ravens periodically returned to areas of high carnivore activity or past kill sites based on anticipated food availability, while primarily foraging elsewhere. Between such revisits, individual ravens ranged far from wolves (median distance: 33 km from GPS-collared wolves, maximum distance: 327 km). Ravens made repeated revisits to specific wolves or wolf packs (Fig. 3A). Notably, the only observed instance of potential following behavior also could be classified as a revisit, as it was a directional movement more than ~60 km toward a wolf territory, followed by a return to the starting point the next day (Fig. 2A). Overall, the frequency of such revisits varied substantially both among and within individuals. Of the 69 tracked ravens, 49 were associated with wolves on at least two different days, with one individual exhibiting associations on 48 separate days. The interval between consecutive revisits ranged widely, with a median of 15 days and a maximum of 363 days. Although some of this variation likely reflects differences in tracking duration (fig. S1), it also highlights pronounced individual differences in revisiting behavior.

Ravens' movements toward wolf kills were often highly directional, covering distances of up to 155 km in a single day (Fig. 3B). Because wolf kills are clustered in particular areas of northern Yellowstone and not randomly distributed, we propose that ravens find kills by relying on spatial memory, possibly represented as a cognitive map of long-term average wolf presence and/or wolf kill abundance. To test this hypothesis, we created a carcass abundance map based on the total number of recorded wolf kills during our study, aggregated into 3-km grid cells (Fig. 3B and fig. S5). The proportion of GPS-tagged ravens visiting a wolf kill was significantly higher in grid cells with greater recorded wolf kill abundance than in areas where kills were previously rare (generalized linear mixed model, with beta-binomial error: estimate = 0.04, SE = 0.01, $P < 0.001$; Fig. 3C; this effect remained strongest when considering wolf kills alone, even relative to models including cougar kills and other ungulate carcasses; table S8). This indicates that ravens may learn and remember areas where wolf kills are abundant and where they are not.

We also compared the directionality of long-distance movements toward wolf kills with movements toward permanent anthropogenic subsidies (such as landfills, sewage ponds, or urban areas), which are ravens' most predictable source of food in the winter (fig. S2 and table S9). Specifically, we analyzed trajectories from ravens' first-time visits to wolf kills (representing low predictability) and compared them with movements toward the most frequently visited permanent anthropogenic subsidies in the study area (very high predictability). Only trajectories containing at least four GPS locations and with path lengths exceeding the median straight-line distance to a resource (7.8 km) were included.

As a simple proxy for movement directionality (*29*), we calculated the average deviation of all GPS fixes from each straight-line path connecting the first recorded location of the day (or the last known location near a resource) to that day's destination—either a wolf kill or an anthropogenic subsidy. We found no significant difference in directionality between movements toward wolf kills (n = 125 trajectories) and those toward anthropogenic subsidies (n = 705 trajectories). However, territorial ravens deviated significantly less from a direct route (back-transformed mean deviation: 1562 ± 139 m SE) than vagrants (2,493 ± 177 m SE), based on trajectories with a median straight-line path length of 27.8 km (range: 7.8 to 170.0 km), as estimated by a generalized linear mixed model with a Gamma error (estimate = 0.46, SE = 0.10, $P < 0.001$; see also table S10). These findings suggest that, despite marked differences in predictability, ravens orient precisely toward both resource types, with territorial individuals moving more directionally than vagrants when anticipating resource locations.

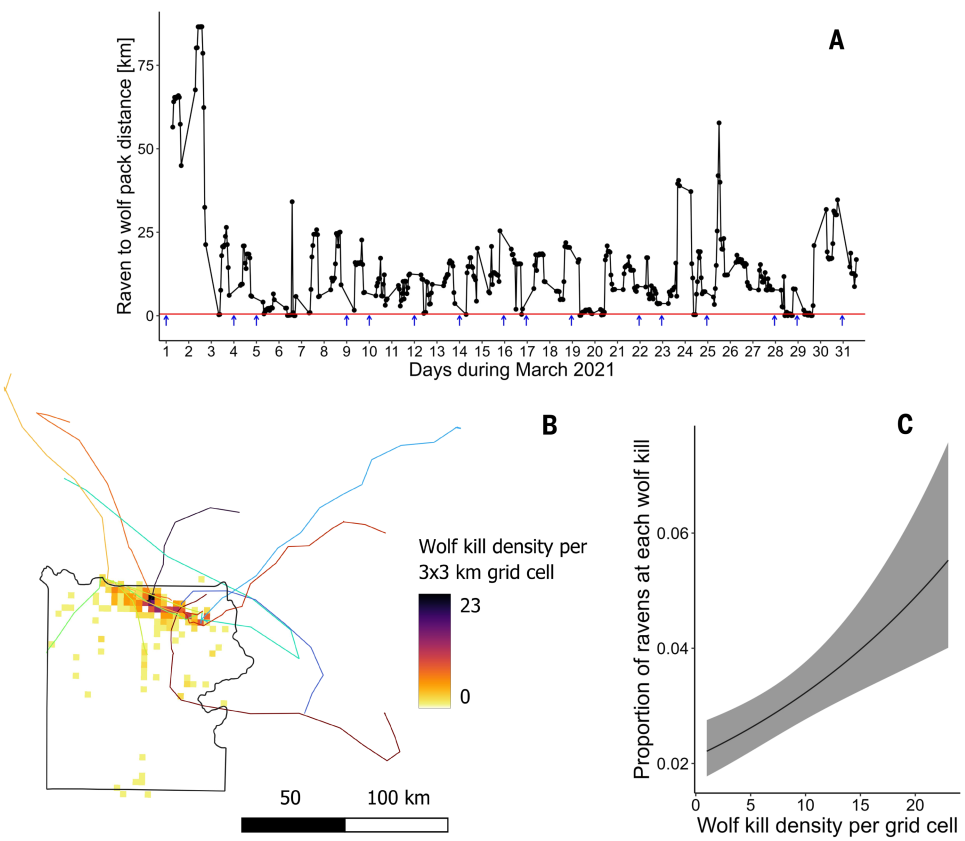

Fig. 3. Ravens' pattern of kill site revisitation. (**A**) Ravens frequently associate with wolves but exploit distant resources in between. The distance between a vagrant raven and a wolf pack in March 2021 is shown. Blue arrows indicate the dates of wolf kills made by the pack. (**B**) Long-distance movements to exploit areas with likely wolf kill presence. Shown are 10 GPS trajectories of ravens (see fig. S5 for additional examples) in which individuals traveled ≥40 km when approaching a wolf kill for the first time (i.e., the distance between their first GPS position of the day and the location of the kill). Colored pixels represent the number of wolf kills in each 3×3 km grid cell during the 2.5-year study period, with darker colors indicating higher kill densities. The black polygon shows the boundaries of Yellowstone National Park. (**C**) The proportion of GPS-tagged ravens exploiting a wolf kill significantly increases with higher kill site abundance in an area. Proportion values are generally low as they refer to all GPS-tagged ravens within a 350 km radius during the first 7 days postmortem.

Navigating a landscape of potential carrion resources

Although the precise location and timing of specific wolf kill events are unpredictable, the broader spatial distribution of kill sites and carrion in general (*30*) is largely driven by landscape features that create predictable hunting grounds. In these areas, predation risk for elk, the main prey of wolves in this system, can be up to 10 times higher than the landscape average (*31*). In winter, these zones—high-risk for prey and high-reward for scavengers—are typically flatter, open, snow-covered grasslands near streams and roads (*26*, *31*), habitats that are easily searched by wide-ranging aerial scavengers such as ravens. By occasionally flying over these areas, ravens may gather information on wolf presence, kill locations, habitat features associated with hunting success, or simply the distribution of bones and other carcass remains in the landscape. By contrast, cougars occupy more topographically rough, less open landscapes, have distinct hunting domains (*16*), and frequently cache their kills; together, these factors reduce ravens' ability to predict and acquire information from cougar presence or kill-site distributions, helping to explain their significantly lower co-occurrence with cougars. Although the current temporal resolution of our GPS tracking data prevents us from analyzing ravens' fine-scale search behavior, we can still assess broader patterns of spatial association. All territorial ravens in this study occupied areas within or near wolf territories, likely giving them more frequent opportunities to acquire information about kill site distributions (fig. S6). This may explain why territorial ravens typically move more directionally than vagrants when anticipating resource locations, even though territorial and vagrant ravens did not differ in their co-occurrence with wolves and cougars or in their use of those kills.

Although the fine-scale search strategies of ravens remain unresolved, their foraging success relies not only on real-time cues (*20*) but also on the predictability of resource-rich areas, and these strategies are not mutually exclusive. The fact that scavengers can feed for several days on the remains of large ungulate carcasses, such as those typically provided by wolves (*32*), alleviates the necessity of being at the right place at the right time. In addition to remembering specific locations to exploit anthropogenic subsidies, ravens also appear to learn that broader landscape areas can be associated with increased carrion availability and/or wolf activity. Consequently, they navigate equally efficiently from distant areas to anthropogenic subsidies as they do to areas with high wolf kill abundance. For local search on a finer scale, ravens likely rely on perceptual cues, including social information from other scavengers (e.g., local enhancement, flight paths, raven vocalizations) (*33*, *34*), as well as short-distance following and monitoring of wolf behavior, such as movement, hunting (*20*), and howling (*19*). The combination of site revisiting and high wolf abundance can make wolf kills a highly predictable food source for ravens and possibly other scavenger species.

Knowledge of a resource landscape by ravens aligns with similar strategies observed in blue whales tracking spring phytoplankton blooms (*35*) or chimpanzees using long-term spatial memory to revisit fruit-bearing trees (*36*). The same mechanism might also be used by other avian scavenger species with high movement capacity (e.g., other corvids, vultures, eagles) to complement their physiological, morphological, and behavioral adaptations for efficient carrion detection.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adz9467
Materials and Methods; Figs. S1 to S6; Tables S1 to S12; MDAR Reproducibility Checklist; References (*38–50*)

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Editor's summary
Many species make their living by scavenging from kills made by other species. Observational knowledge posits that they do this by following predators around. Lorretto *et al*. tested this assumption by tagging ravens, wolves, and cougars in Yellowstone National Park. They found that the ravens weren't following the predators; instead, they regularly returned to sites where they had encountered wolf kills before, like bats returning to known fruiting trees at the right time. These results suggest that scavengers may also use spatial memory of ephemeral resources in their search for food. —Sacha Vignieri

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