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Divergent or convergent: how do forest carnivores use time in the Greater Yellowstone Ecosystem?

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Divergent activity can change the intensity of species interactions, largely affecting species distributions and abundances, and consequently influencing the composition and function of ecological communities. Few assessments of activity patterns have focused questions around different resource constraints or have examined varying time frames when interaction strengths are expected to increase. We evaluated how activity among carnivores and their prey shifted from early to late winter, coinciding with a presumed decrease in food resources for carnivores, and we measured time between species detections within a camera station. Our study species were three forest carnivores—Pacific martens (*Martes caurina*), Rocky Mountain red foxes (*Vulpes vulpes macroura*), coyotes (*Canis latrans*); and two of their prey—American red squirrels (*Tamiasciurus hudsonicus*), and snowshoe hares (*Lepus americanus*). We sampled these species across an extensive network of cameras (n = 107) during the 2014–2017 winter seasons in the Greater Yellowstone Ecosystem, Wyoming. We generated kernel density plots for timing of photographs and calculated the coefficient of overlap among density plots for our predators and prey during early and late winter. Furthermore, we calculated the time-between-detections (i.e., hours) among forest carnivores. We found no consistent trends in time-between-detections across our species pairs. Pacific martens exhibited cathemeral activity that aligned with the peaks in activity of the two prey species. Temporal overlap between coyote and red fox activities was small in early winter, whereas coyotes modified activity in late winter such that they more closely aligned with red foxes. This intraguild convergence of activity may reflect an increase in resource constraints and have consequences for competitive interactions between these two canids. Our study supports the notion that variation in time is an important axis in facilitating coexistence among these forest carnivores and prey species.

Key words: activity patterns, coexistence, forest carnivores, predator–prey, remote cameras, species interactions, temporal resolution

The interactions of sympatric species, particularly predators and prey, affect species distributions and abundances and influence the composition and function of ecological communities (Estes et al. 2011; Ripple et al. 2014). Divergence in space or time can modulate the intensity of interactions among species (Schoener 1974). In multiple predator–prey systems, the role of divergent activity patterns between predator and prey is hypothesized as a significant mechanism allowing prey to avoid predators within risky landscapes (Matassa and Trussell 2014; Kohl et al. 2018). In areas with high pressure (e.g., density or behavioral responses) from predators, prey often respond with intense foraging efforts (Lima and Bednekoff 1999) or forage in risky places during predator downtime (Lima and Dill 1990; Tambling et al. 2015; Kohl et al. 2018). For example, Smith et al. (2019) found that variation in mountain lion (*Puma concolor*) activity provided a temporal refugium for vicuñas (*Vicugna vicugna*) to access high-quality forage during times when mountain lions were not prone to hunting. Indeed, assessing variation in activity across species provides an important lens when evaluating questions of species interactions and coexistence.

Among mammalian carnivores that share foods yet exhibit differences in body size, the smaller species tend to shift activity to avoid competition or predation from the larger species

(Crooks and Soule 1999; Cunningham et al. 2019; Santos et al. 2019; Kemna et al. 2020). In the Serengeti of Africa, Swanson et al. (2016) challenged the established notion that cheetahs (*Acinonyx jubatus*) coexist with lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) only where the larger carnivores have low densities. They found that cheetahs occurred in the same habitat with abundant lions, but only when lions rested. Indeed, temporal variation in animal activity provides opportunities for dampened predation and competition that aid in coexistence (Lima and Dill 1990; Matassa and Trussell 2014; Smith et al. 2019). Nevertheless, evaluating how animals exploit temporal variation under different resource constraints has received less attention (Karanth et al. 2017), yet might provide additional insight regarding patterns of coexistence. For instance, when food is scarce, cheetahs may not have the nutritional flexibility to modulate activity patterns and may need to hunt when lions are active. Examining how animals exploit temporal variation in a resource-based context is warranted.

Temporal interactions among secretive and ecologically cryptic mammals have been assessed using remote cameras (Bridges and Noss 2011; Rowcliffe et al. 2014). Within the past decade, many camera-based studies have yielded insights into patterns of predator–prey interactions (Monterroso et al. 2013; Vilella et al. 2020), interspecific and intraspecific competition (Bu et al. 2016; Karanth et al. 2017; Mengüllüoğlu et al. 2018; Mills et al. 2019), and human–wildlife interactions (Barrueto et al. 2014; Wang et al. 2015). Generally, to estimate activity patterns across a landscape sampled by cameras, the frequency of photo times is used to show the intensity of activity across the day, which can be compared among species to assess temporal overlap (i.e., an index of potential interactions; Ridout and Linkie 2009; Linkie and Ridout 2011). Although insightful, this approach does not explicitly account for spatial variation in species detected across camera stations. Fewer studies have asked focused questions on how two or more species interact within a camera location by using metrics such as the time-between-detections (Vanak et al. 2013). One study found that White-tailed Deer (*Odocoileus virginianus*) waited longer to visit a site after a Florida Panther (*P. c. coryi*), relative to other nonpredator species, and that wild turkeys (*Meleagris gallopavo*) showed the highest probability of visiting a site after a panther in upland habitats (Prat-Guitart et al. 2020). Evaluating targeted questions concerning temporal interactions between species within a camera provides a complement to conventional approaches when assessing how species use time.

We assessed the use of time among three co-occurring forest carnivores with varying temporal resolutions in the mountains of the Greater Yellowstone Ecosystem (GYE). Pacific martens (*Martes caurina*), Rocky Mountain red foxes (*Vulpes vulpes macroura*; Cross et al. 2018; Quinn et al. 2022), and coyotes (*Canis latrans*) all prey on American red squirrels (*Tamiasciurus hudsonicus*) and snowshoe hares (*Lepus americanus*), yet consume other prey as well. Temporal divergence in hunting times between the predators may reduce intraguild competition and predation within the GYE. Martens are mostly restricted to forest habitats (e.g., late-successional conifer stands with an abundance of large downed logs and snags; Buskirk and Ruggiero 1994; Powell et al. 2003). Mountain red foxes are a cold-adapted species, occurring in boreal and montane habitats (Aubry 1983; Swanson et al. 2005; Aubry et al. 2009) and exploit more mesic and sagebrush (*Artemisia* spp.) habitats in winter (Van Etten et al. 2007). Coyotes are behaviorally flexible and occupy a wide range of landscapes (Laliberte and Ripple 2004). Even though habitat preferences differ among these predators, their diets narrow as winter progresses, potentially increasing spatiotemporal overlap and competition among the predators. Rocky Mountain red foxes have a generalist diet consuming subnivean prey, including voles (Arvicolinae) and supranivean prey, including hares (*Lepus* spp.), carrion, and seeds of whitebark pine (*Pinus albicaulis*; Cross and Crabtree 2021). As the snow deepens, however, red foxes become less able to pounce through the snow to capture subnivean prey (Lindström et al. 1994; Willebrand et al. 2017) and consume more hares and excavate ungulate carrion. Forest-dwelling coyotes consume voles primarily from early to mid-winter, switching to nearly 75% carrion and supplementing with hares for the remainder of the season (Crabtree and Sheldon 1999; Bekoff and Gese 2003). In contrast, martens use the snow surface during the entire winter to prey upon hares. (Hargis and McCullough 1984; Thompson and Colgan 1990; Andruskiw et al. 2008) and to consume carrion (Powell et al. 2003), but martens also access the subnivean zone in pursuit of small mammals, visiting *Tamiasciurus* spp. middens frequently (Zielinski et al. 1983; Sherburne and Bissonette 1994; Powell et al. 2003). These three forest carnivores similarly depend on ungulate biomass/carrion in late winter as resources become constrained. In the mountains of the GYE, ungulate biomass is stable or decreasing through the winter due to ungulate migration out of the mountains in early winter (Middleton et al. 2013; Rickbeil et al. 2018; Sawyer et al. 2019).

As winter progresses and snow depth increases in the GYE, access to subnivean small mammals becomes increasingly limited for supranivean forest carnivores. We hypothesize (H_1) that supranivean predators increase temporal overlap with red squirrels and snowshoe hares in late winter relative to early winter as access to other foods decreases. As for intraguild interactions, we hypothesize (H_2) that red foxes and coyotes reduce temporal partitioning in late winter, but that (H_3) martens exhibit similar activity patterns in early and late winter because they can access the subnivean zone and thus experience less resource constraint relative to the canids. At a finer temporal resolution, we hypothesize (H_4) that red foxes display delayed time-to-detection after a coyote detection because coyotes are a larger canid with the potential to displace or kill red foxes (Sargeant et al. 1987; Gosselink et al. 2003; Prugh and Sivy 2020). We expected coyotes to be indifferent to red foxes, and thus display a shorter time interval between detections relative to a coyote followed by a red fox sequence. Lastly, we hypothesize (H_5) no effect of the canids on martens or vice versa, largely because martens have demonstrated indifference to risk from stronger competitors such as fishers (*Pekania pennanti*; Kautz et al. 2021). Collectively, our work extends the popular assessment of

activity patterns into a resource-based context with the aim of refining our understanding of how forest carnivores exploit time.

Materials and Methods

Study area and data collection.—Our study occurred in the mountains of the GYE of Wyoming, United States (Fig. 1). The GYE is situated in the central Rocky Mountains and covers approximately 38,900 km^2, of which 90% was federal lands consisting of: Yellowstone and Grand Teton national parks; portions of Shoshone, Bridger-Teton, and Caribou-Targhee national forests; the National Elk Wildlife Refuge; and Bureau of Land Management holdings (BLM 2016). The elevation ranged from 1,340 to 4,205 m, with an average of 2,616 m. Sagebrush and grassland steppe dominated at low elevations; forests of Lodgepole Pine (*P. contorta*), Douglas-Fir (*Pseudotsuga menziesii*), Engelmann Spruce (*Picea engelmannii*), and Quaking Aspen (*Populus tremuloides*) dominated at mid-elevations; Whitebark Pine, subalpine vegetation, sparse vegetation, and barren terrain dominated at high elevations (Despain 1990; LANDFIRE 2021); while *Salix* spp. and other riparian vegetation occupied the drainages throughout the elevation gradient. Snow accumulation generally started in early November and ended in early May, and snow depth averaged 1 m during our study (NOHRSC 2004).

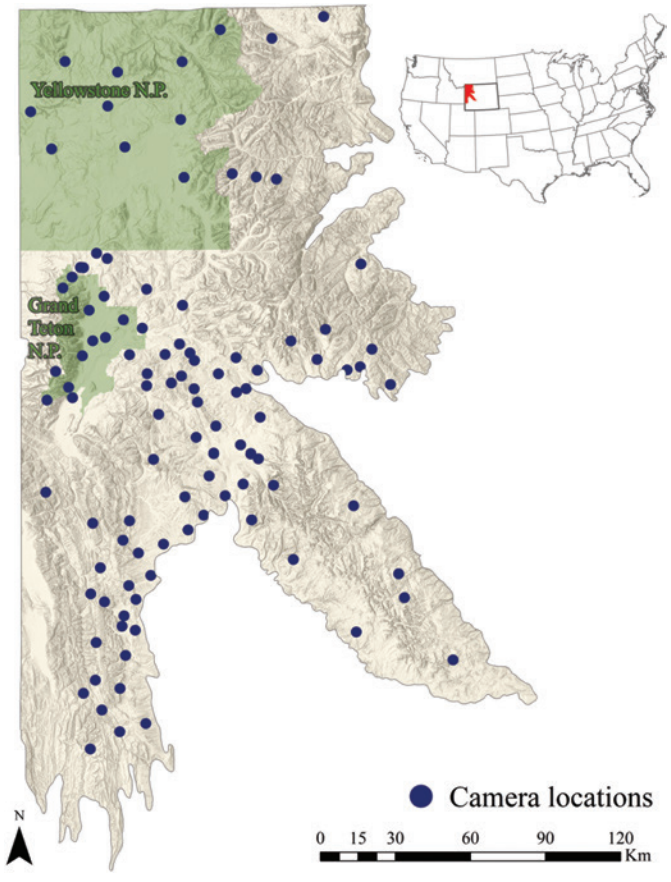

Fig. 1.—Camera locations (n = 107) across the Greater Yellowstone Ecosystem, Wyoming, during the winters of 2014–2015 through 2016–2017.

We collected photographs throughout the winters of 2014–2015 through 2016–2017 (Fig. 1). We deployed 107 cameras (Reconyx Hyperfire, models PC 800, PC 850, or PC 900; Reconyx, Holmen, Wisconsin) based on the expected habitat suitability of forest carnivores and expert opinion to increase the likelihood of photographing the forest carnivore assemblage. Camera elevations ranged from 1,933 to 3,231 m and averaged 2,593 m (±294 m). We set cameras for sensitivity = high; pictures per trigger = three or five; and picture intervals = 1 or 3 s. Each camera was set 1.5 m above the mean annual snowfall on the northern side of a tree with attractants on an adjacent tree, mainly in mature, multistored spruce/fir and lodgepole pine forest types. Attractants varied including: a half Beaver (*Castor canadensis*) carcass: a leg of roadkill Mule Deer (*O. hemionus*); Caven's Gusto (Minnesota Trapline Products, Pennock, Minnesota) scent lure (Lukacs et al. 2020); and visual objects (e.g., pie plates, compact discs, and feathers). Cameras placed at inaccessible locations (e.g., winter access restrictions, Yellowstone National Park restrictions, unsafe—avalanche risk, or too remote) were deployed with an automatic long-call scent lure dispenser and a Cow (*Bos taurus*) femur. The replacement of bait, exchange of batteries, and memory card swap ranged from zero times in the survey season to once per month, with the majority of cameras visited and rebaited with a median rate of 39 days. We archived and identified camera photos using Colorado Parks and Wildlife Photo Warehouse (Ivan and Newkirk 2016).

Diel activity patterns.—We assessed overlap in diel activity between forest carnivores and their prey and among all three carnivores during early and late winter. We characterized early winter as 1 November to 31 January and late winter as 1 February to 30 April, which was related to snow depth and ensured a relatively even split of our detection of focal species across cameras (early = 47,320 detections, late = 78,952 detections). Within the elevation range of our cameras, snow depth was lower during the early winter (0.66 m, interquartile range [IQR] = 0.51–0.82 m) relative to the late winter (1.26 m, IQR = 0.83–1.67 m; Fig. 2). The daily activity of terrestrial animals is often associated with astronomical events (e.g., sunrise, sunset, and light intensity; Aschoff 1960; Halle and Stenseth 2000; Caravaggi et al. 2018), which vary across time and location. In the GYE, the maximum variation in sunrise and sunset (i.e., between the earliest and latest sunrise/sunset) was approximately 2.5 h during our study. To account for variation in daylight length through the annual orbital cycle, we converted clock time to sun time for all detections. We standardized our detections by transforming clock time into a relative sun time corresponding with sunrise and sunset based on the date and latitude (latitude: 43.7, longitude: −110.1) centroid of the GYE, and the relative sunrise and sunset were set at 0600 and 1800 using the 'sunTime' function in the *overlap* package in R (Nouvellet et al. 2012; R Core Team 2019; Meredith and Ridout 2020). For example, 0600 MST on 21 December and 30 April would equal approximately 1.27 and 1.59 sun time, respectively, illustrating an increased difference between

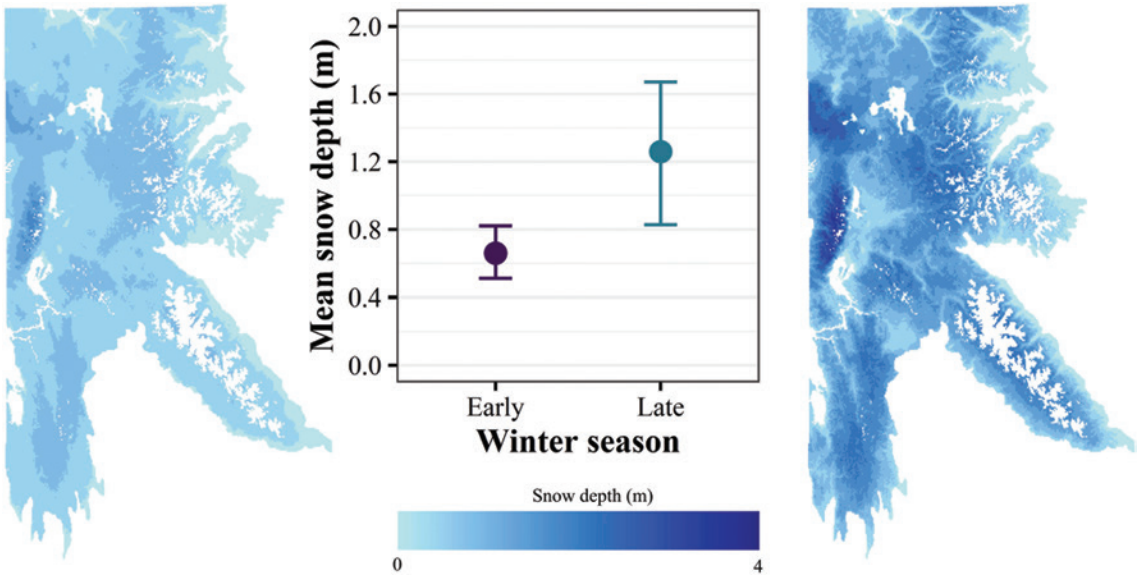

Fig. 2.—Mean (error bars are interquartile range; IQR) snow depth was computed from the minimum (1,933 m) to maximum (3,231 m) elevation of cameras deployed in the winters of 2014–2015 through 2016–2017 in the Greater Yellowstone Ecosystem, Wyoming. White areas on the maps indicate locations outside the elevation ranges we assessed. The mean snow depth from 1 November to 30 April during our study period was 0.99 m. The mean snow depth for early winter (1 November to 31 January; 0.66 m, IQR = 0.51–0.82 m) was statistically lower ($P < 0.001$) than late winter (1 February to 30 April) mean snow depth (1.26 m, IQR = 0.83–1.67 m).

biological sunrise and 0600 as the season progresses from 21 December to 30 April. Therefore, as sunrise and sunset change throughout the season, so does our sun time, whereas clock time would remain the same.

To estimate overlap in activity between species across a 24-h period and assess how overlap shifted from early to late winter, we followed a two-step procedure described by Ridout and Linkie (2009). First, we estimated activity curves for each species during early and late winter seasons using a nonparametric kernel density estimator. These curves characterized the densities of activity across the 24-h period. Second, we calculated the coefficient of overlap, Δ (i.e., the degree of overlap in daily activity curves), between forest carnivores and their prey, as well as among all forest carnivores, using the *overlap* package. The coefficient of overlap is defined as the area under the activity curves, estimated by taking the minimum density function between the two curves being compared at each point in time (Ridout and Linkie 2009). The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap; Linkie and Ridout 2011) and is used to investigate potential interactions between species in time (Farris et al. 2016; Farmer et al. 2021).

To provide reference values that aid in biological interpretation, we generated three commonly observed, yet distinct activity patterns (cathemeral, nocturnal, and diurnal) and calculated the coefficient of overlap. We defined cathemeral as a species being active from 0 to 2400, nocturnal as being active from 1800 to 0600, and diurnal as being active from 0600 to 1800. Under these simplified scenarios, we calculated a coefficient of overlap between diurnal and nocturnal species, cathemeral and nocturnal species, and two species with nocturnal activity using the minimum suggested sample size ($n = 100$; Lashley et al. 2018) to estimate the coefficient of overlap. To generate two species with nocturnal activity, yet somewhat different density curves, we established a baseline nocturnal activity curve and varied the second curve by offsetting the nocturnal activity. The coefficient of overlap across scenarios was: (1) diurnal and nocturnal Δ = 0.22; (2) cathemeral and nocturnal Δ = 0.59; and (3) nocturnal and nocturnal Δ = 0.93 (Fig. 3). This assessment demonstrated that the coefficient of overlap in natural settings will likely express a range narrower than from 0 to 1. Additionally, we used this exercise to establish our biological reference points and suggest that an overlap coefficient ≥0.60 is *high* overlap, between 0.20 and 0.60 is *moderate* overlap, and ≤0.20 is *low* overlap.

To accurately estimate activity curves, Ridout and Linkie (2009) indicated that the nonparametric estimator Δ_1 performs best with small sample sizes (i.e., $n \leq 75$), while Δ_4 is appropriate for large sizes ($n \geq 75$). All of our species had a minimum of 1,000 detections (defined as ≥1 individual of the same species per photo) in both early and late winter (Table 1); therefore, we used Δ_4 throughout our analyses. Lastly, for each coefficient of overlap, we obtained 95% confidence intervals from 1,000 bootstrap samples (Linkie and Ridout 2011).

To complement our assessment of overlap in activity (H_{1-3}), we also tested whether species expressed statistically different distributions of activity (Frey et al. 2017). We evaluated whether two activity curves were different using the Watson U^2 test (Watson 1962; Zar 2010) from the *CircStats* package in R (Agostinelli and Lund 2018; R Core Team 2019). The Watson U^2 test determined whether the circular distribution in activity among each pair of species was statistically similar. We also evaluated whether the distribution in activity differed within a species from early winter to late winter. This assessment helped us differentiate which species

demonstrated seasonal shifts in activity versus those that remained stable.

Time-between-detections.—To evaluate finer-scale (i.e., hourly) questions of temporal interactions ($H_{4–5}$), we used a time-between-detections approach. We defined time-between-detections as the difference in time of a focal species (e.g., Red Fox = t_0) followed by a subsequent focal species (e.g., Marten = t_1) at a single camera. Time-between-detections were calculated in both directions for all three forest carnivores (e.g., carnivore 1–carnivore 2, carnivore 2–carnivore 1) to determine whether there was evidence of aversion or indifference among species. Due to the small sample sizes of sequential detections across species in the early and late winter seasons (e.g., we observed as few as two sequences), we evaluated time-between-detections across the entire winter season. We restricted the time-between-detections to 168 h, or 7 days, because we expected chemosensory cues to fade or become less detectable over time in varying weather conditions (Parsons et al. 2018). We expected that as the time-between-detections narrowed, the stronger would be the chemosensory cues, which would result in stronger behavioral patterns. Therefore, we examined how varying extents of time (168, 72, and 24 h) affected patterns of median time-between-detections. Because time-between-detections were heavily right-skewed, we calculated the median time-between-detections and an associated nonparametric confidence interval (i.e., median ± 1.58 × IQR/$\sqrt{n}$; Chambers et al. 1983). If nonparametric confidence intervals did not overlap, we concluded there was evidence of a statistical difference.

Results

We recorded 126,272 total detections of Pacific martens, Rocky Mountain red foxes, coyotes, red squirrels, and snowshoe hares across all 107 cameras and all three winters. These target species represented 65% of the total detections, while the other notable species included black-billed magpies (*Pica hudsonia*; ~25%), Clark's nutcrackers (*Nucifraga columbiana*; ~4%), common ravens (*Corvus corax*; ~2%), bobcats (*Lynx rufus*; <1%), black bears (*Ursus americanus*; <1%), and Moose (*Alces alces*; <1%). The naïve occupancy rate (i.e., the total number of cameras with at least one detection divided by the total number of cameras) for our focal species was greatest for Pacific martens (0.96) and the lowest for snowshoe hares (0.52; Table 1). Of the three forest carnivores, martens had the highest number of detections (58,322), followed by Rocky Mountain red foxes (46,703) and coyotes (9,472). For prey species, red squirrels had 7,744 detections and snowshoe hares had 4,031 detections. Detections of all five species were about 1.7 times more prevalent in late winter (78,952 detections) compared with early winter (47,320 detections; Table 1). Detections of all five species ranged in elevation from 1,933 to 3,231 m (Table 1).

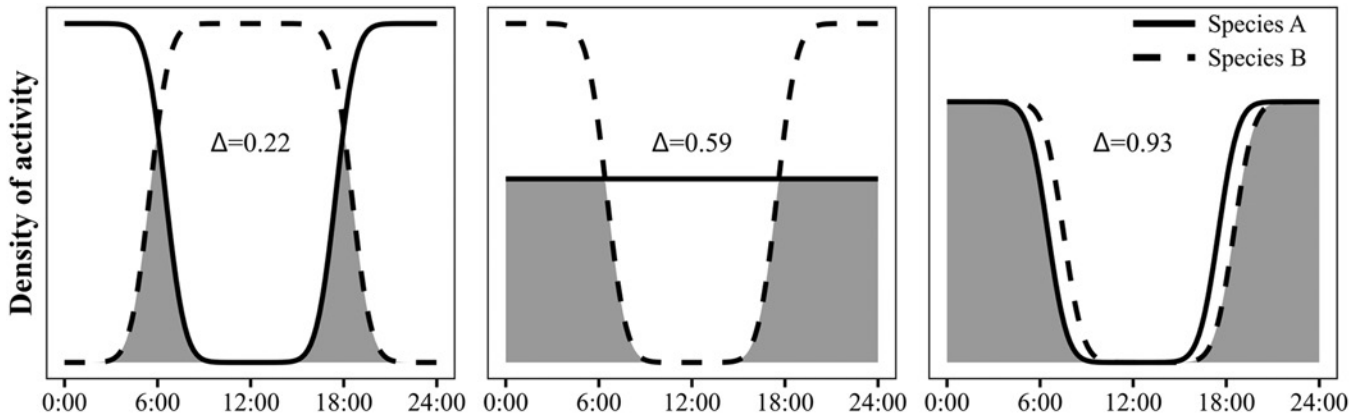

Fig. 3.—Simulated biological scenarios of different activity curves among three pairs of species. The first panel represents two opposing activities from nocturnal and diurnal species. The second panel represents a species with constant activity, and a species with nocturnal activity. The third panel illustrates two species with similar diel activity. All three panels indicate that some level of activity occurs between species regardless of diel activity.

Table 1.—The total number of pictures taken, total sites where species were detected, and the naïve occupancy rate (i.e., the total number of cameras with at least one species detection divided by the total number of cameras) from winter surveys during 2014–2015, 2015–2016, and 2016–2017 in the Greater Yellowstone Ecosystem, Wyoming. The total number of camera stations was 107. Detections were summarized by early (1 November to 31 January) and late (1 February to 30 April) winter seasons. Camera elevation (interquartile range; IQR) was calculated by averaging the elevation of each camera where the focal species was detected from 1 November to 30 April.

Species	Total photos	Total sites detected	Naïve occupancy	Camera elevation (m), (IQR)	Early winter detections	Late winter detections
Pacific Marten	58,322	103	0.96	2,592 (383)	26,635	31,687
Rocky Mountain Red Fox	46,703	95	0.89	2,600 (388)	15,885	30,818
Coyote	9,472	64	0.60	2,544 (311)	1,243	8,229
American Red Squirrel	7,744	65	0.61	2,592 (363)	2,108	5,636
Snowshoe Hare	4,031	56	0.52	2,641 (378)	1,449	2,582

Diel activity patterns.—We observed substantial variation in activity across forest carnivores and their prey. Red squirrels were mostly diurnal, exhibiting a peak in activity midday (Fig. 4). From early to late winter, red squirrel activity stayed similar, but the peak in activity shifted from midday to early morning (Table 2; Fig. 4). In contrast, snowshoe hares were primarily nocturnal, with a similar density of activity in the late evening through early morning (Fig. 4) and a high overlap (Δ = 0.89; Table 2). Among forest carnivores, patterns in activity from early to late winter were quite similar for martens and red foxes, which was illustrated by very high overlap coefficients (Δ = 0.90 and 0.83, respectively; Table 2; Fig. 4). In contrast, coyotes exhibited distinct differences in activity from early to late winter with sporadic activity changes throughout the diel period, which resulted in a lower overlap coefficient (Δ = 0.64; Table 2; Fig. 4). Across forest carnivores, red foxes displayed more nocturnal activity, martens exhibited cathemeral activity throughout the 24-h period, and coyotes displayed peaks in activity during both day and night hours (Fig. 4).

Overlap in activity between forest carnivores and their prey differed for all pairs of species between early and late winter (Figs. 5 and 6). In general, there was more overlap among forest carnivores and snowshoe hares (Δ = 0.45–0.75) than red squirrels (Δ = 0.20–0.46; Figs. 5 and 6). Consistent with expectations of declining access to alternative prey through increasing snow depth (Fig. 2), the overlap in activity with red squirrels for red foxes, martens, and coyotes all increased from early to late winter (supporting H_1; Fig. 5). Martens and coyotes displayed the highest overlap with red squirrels, while red foxes showed the lowest overlap in activity (Fig. 5). In contrast, the overlap in activity with snowshoe hares for martens and red foxes declined from early to late winter (refuting H_1 and

Table 2.—Overlap of activity curves within species to assess variation between early (1 November to 31 January) and late (1 February to 30 April) winter seasons in the Greater Yellowstone Ecosystem, Wyoming. Symbol Δ represents the coefficient of overlap. A Δ = 0 denotes no temporal overlap, whereas a Δ = 1 denotes complete overlap. Confidence intervals (CIs) were calculated at 95% using 1,000 bootstrap samples. The Watson's U^2 test evaluated if early and late winter activity curves within each species were statistically different.

	Early winter to late winter	
	Watson's U^2 test	Coefficient of overlap
Pacific marten	U = 1.23, P < 0.001	Δ = 0.90, CI = 0.90–0.91
Rocky Mountain red fox	U = 0.37, P < 0.01	Δ = 0.83, CI = 0.82–0.84
Coyote	U = 0.56, P < 0.001	Δ = 0.64, CI = 0.61–0.66
American red squirrel	U = 0.09, P > 0.10	Δ = 0.62, CI = 0.60–0.64
Snowshoe hare	U = 0.105, P > 0.10	Δ = 0.89, CI = 0.86–0.91

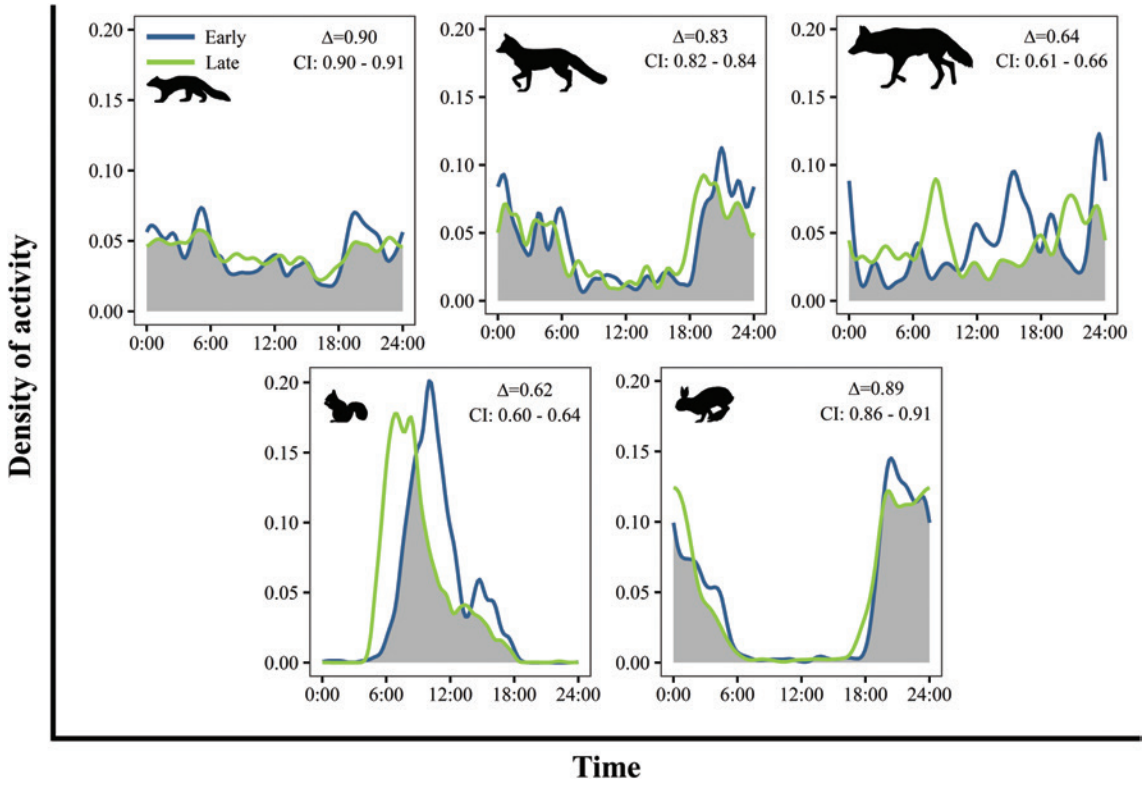

Fig. 4.—Kernel density estimate of daily activity patterns across solar time within each focal species: Pacific martens (*Martes caurina*); Rocky Mountain red foxes (*Vulpes vulpes macroura*); coyotes (*Canis latrans*); American red squirrels (*Tamiasciurus hudsonicus*); and snowshoe hares (*Lepus americanus*) during the winters of 2014–2015 through 2016–2017 in the Greater Yellowstone Ecosystem, Wyoming. The dark (blue) line represents the early (1 November to 31 January) winter season, and the light (green) line represents the late winter (1 February to 30 April) season. The area of overlap between the two species is denoted in gray. Symbol Δ represents the coefficient of overlap—Δ = 0 denotes no temporal overlap, whereas a Δ = 1 denotes complete overlap. Confidence intervals were calculated at 95% using 1,000 bootstrap samples.

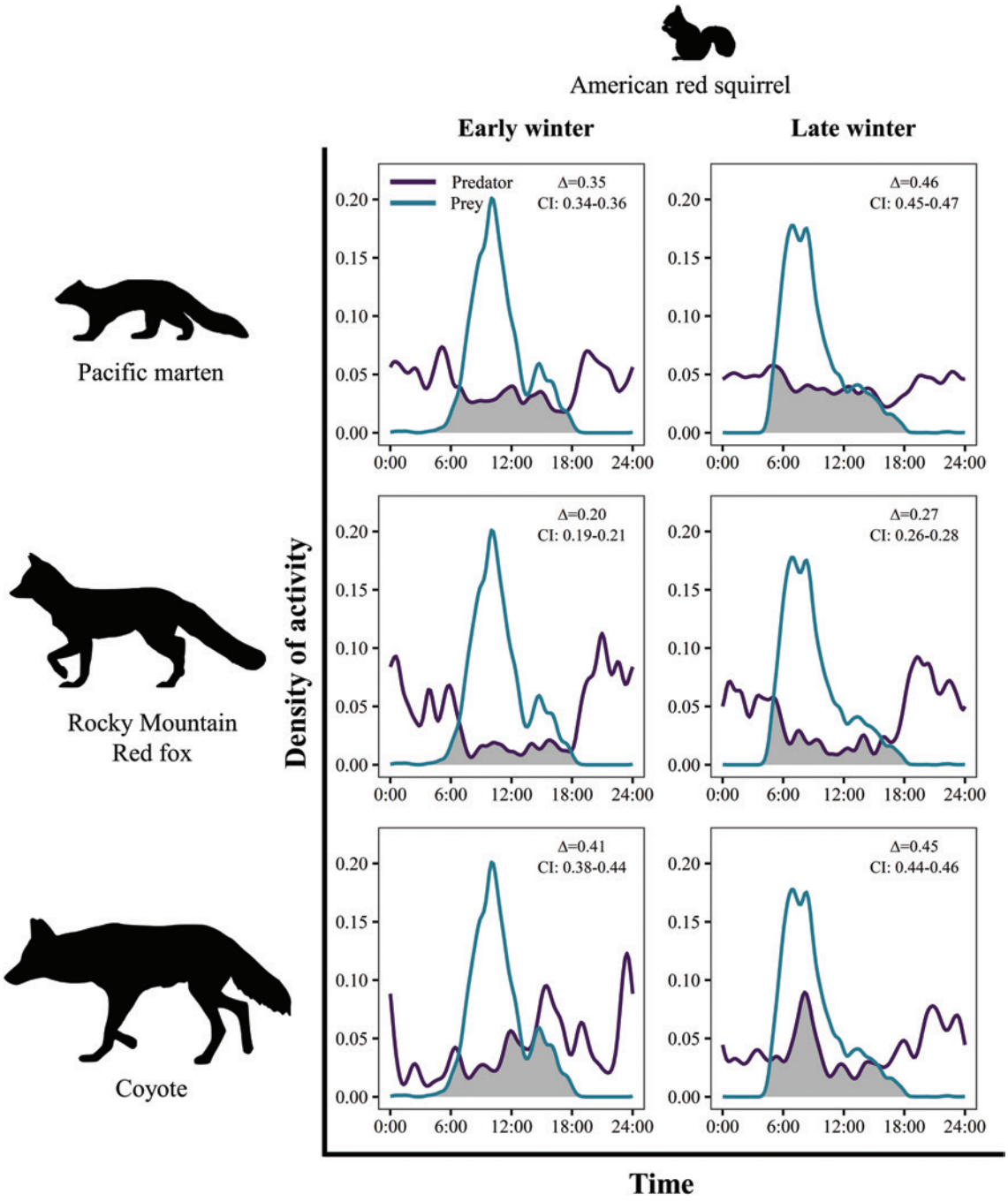

Fig. 5.—Kernel density estimate of daily activity patterns across solar time for forest carnivores and American red squirrels (*Tamiasciurus hudsonicus*) during the winters of 2014–2015 through 2016–2017 in the Greater Yellowstone Ecosystem, Wyoming. The early winter season represents 1 November to 31 January and late winter season represents 1 February to 30 April. The dark (purple) line represents the corresponding forest carnivore species, and the light (turquoise) line represents red squirrels. The area of overlap between the two species is denoted in gray. Symbol Δ represents the coefficient of overlap—Δ = 0 denotes no temporal overlap, whereas a Δ = 1 denotes complete overlap. Confidence intervals were calculated at 95% using 1,000 bootstrap samples.

H_3; Fig. 6); yet, despite this decline, the total overlap in late winter with snowshoe hares remained greater than the overlap with red squirrels (Figs. 5 and 6). Nonetheless, overlap between snowshoe hares and coyotes increased from early to late winter (supporting H_1; Fig. 6), which appeared to be mediated primarily by coyotes altering their activity rather than snowshoe hares (Fig. 4). Across all combinations of forest carnivores and prey, activity curves were statistically different between predator and prey (Table 3).

Among forest carnivores, two species pairs increased in overlap from early to late winter, while overlap between marten and red fox remained unchanged. The overlap in activity between red foxes and coyotes increased from early to late winter (supporting H_2; Fig. 7). This increase appeared to be largely associated

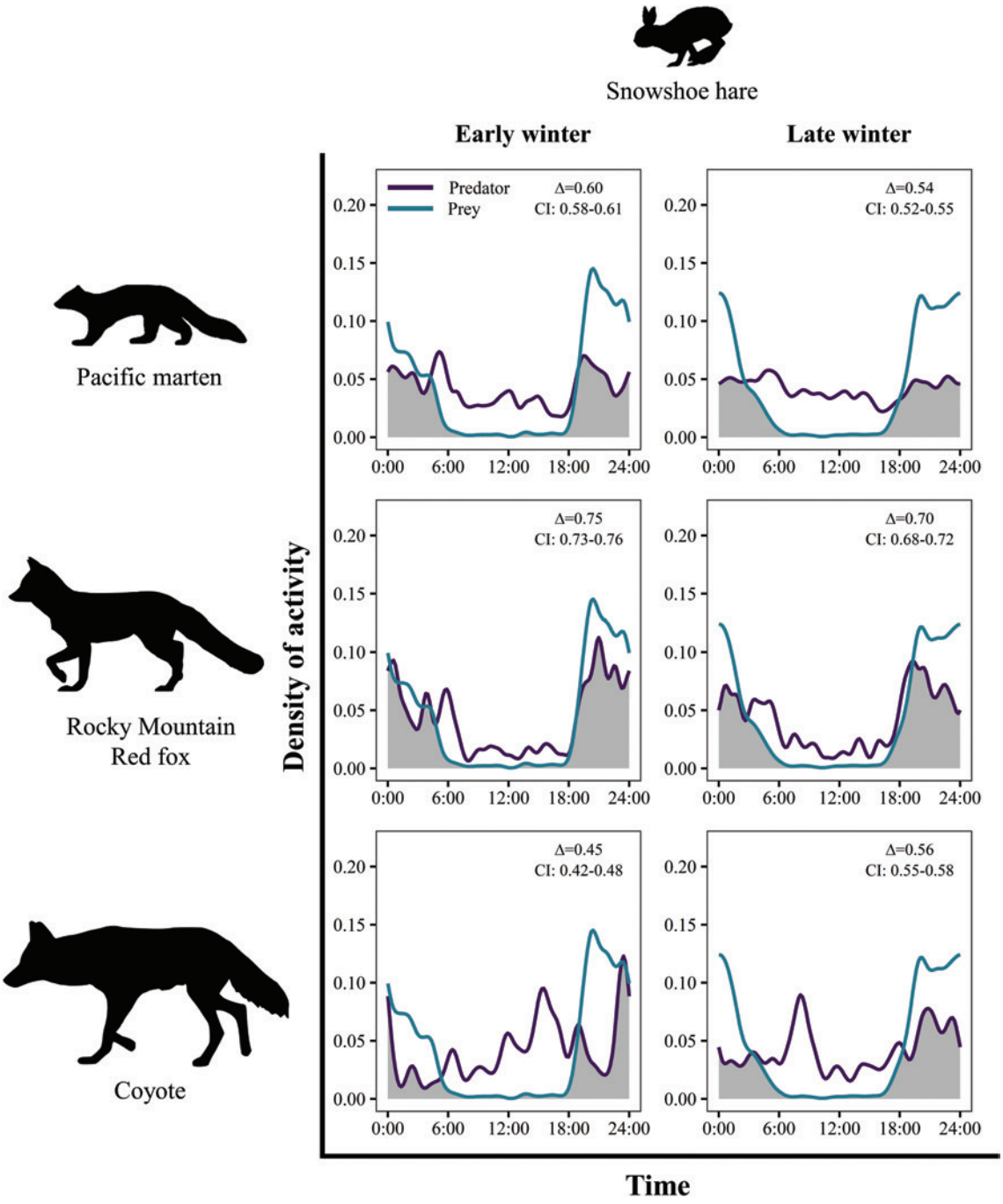

Fig. 6.—Kernel density estimate of daily activity patterns across solar time for forest carnivores and snowshoe hares (*Lepus americanus*) during the winters of 2014–2015 through 2016–2017 in the Greater Yellowstone Ecosystem, Wyoming. The early winter season represents 1 November to 31 January and late winter season represents 1 February to 30 April. The dark (purple) line represents the corresponding forest carnivore species, and the light (turquoise) line represents snowshoe hares. The area of overlap between the two species is denoted in gray. Symbol Δ represents the coefficient of overlap—Δ = 0 denotes no temporal overlap, whereas a Δ = 1 denotes complete overlap. Confidence intervals were calculated at 95% using 1,000 bootstrap samples.

with coyotes shifting their activity from the afternoon to early morning and night, while red fox activity remained comparatively more stable (Table 2; Fig. 4). Similarly, the overlap in activity between coyotes and martens increased from early to late winter (Fig. 7); again, likely from shifts in coyote activity as marten activity remained consistent (supporting H_3; Table 2; Fig. 4). In both early and late winter, all carnivores exhibited statistically different activity patterns (coyote–fox—early: U = 0.76, $P < 0.001$, late: U = 1.30, $P < 0.001$; coyote–marten—early: U = 0.66, $P < 0.001$, late: U = 1.66, $P < 0.001$; fox–marten—early: 2.29, $P < 0.001$, late: U = 13.58, $P < 0.001$).

Time-between-detections.—Contrary to our hypotheses (H_4 and H_5), we discovered the median time-between-detections within a camera station was similar for nearly all pairings of

Table 3.—Differences in temporal activity between forest carnivores and their prey in early (1 November to 31 January) and late (1 February to 30 April) winter in the Greater Yellowstone Ecosystem, Wyoming. The Watson's U^2 test evaluated if early and late winter activity curves between all combinations of forest carnivores and their prey were statistically different.

	Early winter		Late winter	
	Red squirrel	Snowshoe hare	Red squirrel	Snowshoe hare
Pacific marten	$U = 2.78$, $P < 0.001$	$U = 3.70$, $P < 0.001$	$U = 3.35$, $P < 0.001$	$U = 4.01$, $P < 0.001$
Rocky Mountain red fox	$U = 1.77$, $P < 0.001$	$U = 2.37$, $P < 0.001$	$U = 1.73$, $P < 0.001$	$U = 3.58$, $P < 0.001$
Coyote	$U = 2.17$, $P < 0.001$	$U = 2.88$, $P < 0.001$	$U = 2.43$, $P < 0.001$	$U = 3.27$, $P < 0.001$

forest carnivores (Fig. 8). We found no statistical difference in the time-between-detections among our forest carnivore sequences, refuting our expectations (H_4 and H_5). The only consistent pattern we observed was a general increase in time-between-detections as we increased the temporal extent (from 24 to 168 h), which was expected due to sampling variation.

Discussion

Divergent activity patterns are hypothesized as a significant mechanism facilitating coexistence by allowing prey to avoid predators, or subordinate predators to avoid dominant predators within risky landscapes (Crooks and Soule 1999; Matassa and Trussell 2014; Kohl et al. 2018; Cunningham et al. 2019). We evaluated how forest carnivores and their prey use time during the winter months in the mountains of the GYE. Our assessment extended conventional camera-based approaches by (1) evaluating how activity patterns among carnivores changed with reduced access to food resources, and (2) controlling for location and assessing patterns of temporal attraction or avoidance between species within a camera station. We expected access to food resources for carnivores (especially the supranivean carnivores red fox and coyote) to become more limited in late winter, associated with deeper snow (Fig. 2) and ungulate migration out of the mountains in early winter (Middleton et al. 2013; Sawyer et al. 2019). We demonstrated that late winter conditions likely reduce access to subnivean and mobile resources through the accumulation of deep snow, and that all carnivore species increased their overlap in activity with red squirrels in late winter. In contrast, martens and red foxes decreased their overlap in activity with snowshoe hares from early to late winter, yet the overlap in activity with snowshoe hares still remained higher than overlap with red squirrels in late winter. Coyotes exhibited the most substantial shift in activity from early to late winter, which increased overlap in activity with both prey species, as well as red foxes and martens. This temporal convergence may have consequences on competitive interactions between predators by increasing the probability of a coyote encountering a fox or marten, which could have implications on resource competition, interference competition, and/or intraguild predation. Nevertheless, snowshoe hares and red squirrels always had some degree of temporal relief from predators in that overlap in activity curves was consistently ≤0.75. Conversely, as winter progressed, temporal relief was constrained within predators in that overlap in activity was >0.75 in late winter for all three predators. Our work suggests that variation in use of time plays an important role in facilitating the coexistence of forest carnivores and their prey, and that later winter conditions could increase intraguild competition within the high-elevation mountains of the GYE.

Carnivore insights.—Our study has contributed to investigating red fox–coyote interactions in the mountains of western North America (Dekker 1989; Gese et al. 1996; Fuhrmann 1998; Perrine 2005; Klauder et al. 2021), which was our main focus among carnivores because these two species are supranivean and have been observed to compete for resources. As we hypothesized, red fox and coyote activity overlap increased in late winter (Fig. 7), consistent with a resource constraint. In our study, red fox activity remained nocturnal and crepuscular across early and late winter, but the density of activity intensified at dawn and dusk during late winter. Coyotes illustrated a significant shift between early and late winter, shifting diurnal activity peaks in the afternoon to the morning and increasing nocturnal activity. In the northern range of Yellowstone National Park, Fuhrmann (1998) found that red foxes demonstrated almost exclusively nocturnal and crepuscular activity, and coyotes were more active during the day in winter. Further, Aubry (1983) found similar crepuscular patterns in Cascade red foxes (*V. v. cascadensis*) in Washington. Although diurnally active, coyotes in our study illustrated a sharp change from primarily diurnal and crepuscular in early winter to cathemeral activity in late winter. Cathemeral activity in coyotes has been seen in Denali National Park and Preserve, Alaska (Klauder et al. 2021).

As the winter progresses, the difficulty to pounce through layers of hardening snow to gain access to small mammals in the subnivean zone can increase, limiting prey availability to mainly ungulate carrion left by larger carnivores or other forms of mortality (e.g., starvation, hunter loss, senescence, or winter conditions; Fuhrmann 1998; Gese et al. 2013; Sivy et al. 2017). Ungulate carrion, however, may become limited over the course of winter in high-elevation environments if ungulate migrations out of the system occur, as was generally the case in our high-elevation sampling area. Additionally, carrion in this context is generally a subnivean resource requiring excavation, but is stationary versus mobile small mammals. Fewer food options create resource constraints and may increase the strength of intraguild competition, assuming one of the species does not seasonally move. Prior to gray wolf (*C. lupus*) reintroduction in Yellowstone National Park, Gese et al. (1996) found that coyotes tolerated foxes in the absence of an ungulate carcass; however, in the presence of a carcass, a pack of coyotes (often not a single coyote) deterred and displaced foxes. Other work has indicated that red fox home ranges do not coincide

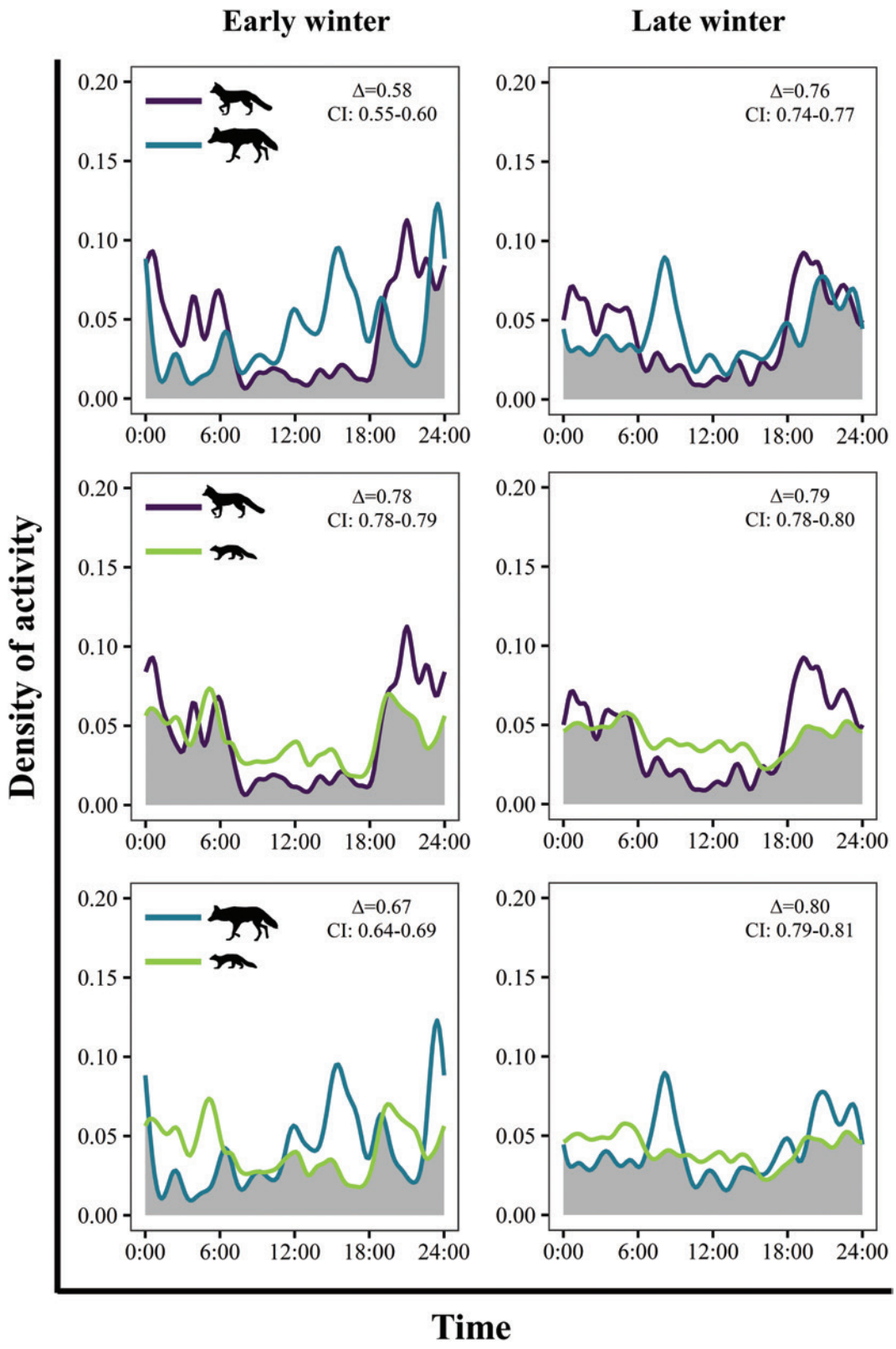

Fig. 7.—Kernel density estimate of daily activity patterns across solar time for forest carnivores during the winters of 2014–2015 through 2016–2017 in the Greater Yellowstone Ecosystem, Wyoming. Forest carnivores included: Pacific martens (M*artes caurina*); Rocky Mountain red foxes (*Vulpes vulpes macroura*); and coyotes (*Canis latrans*). The early winter season represents 1 November to 31 January and late winter season represents 1 February to 30 April. The dark (purple) line represents red foxes, the intermediate (turquoise) line represents coyotes, and the light (green) line represents martens. The area of overlap between the two species is denoted in gray. Symbol Δ represents the coefficient of overlap—Δ = 0 denotes no temporal overlap, whereas a Δ = 1 denotes complete overlap. Confidence intervals were calculated at 95% using 1,000 bootstrap samples.

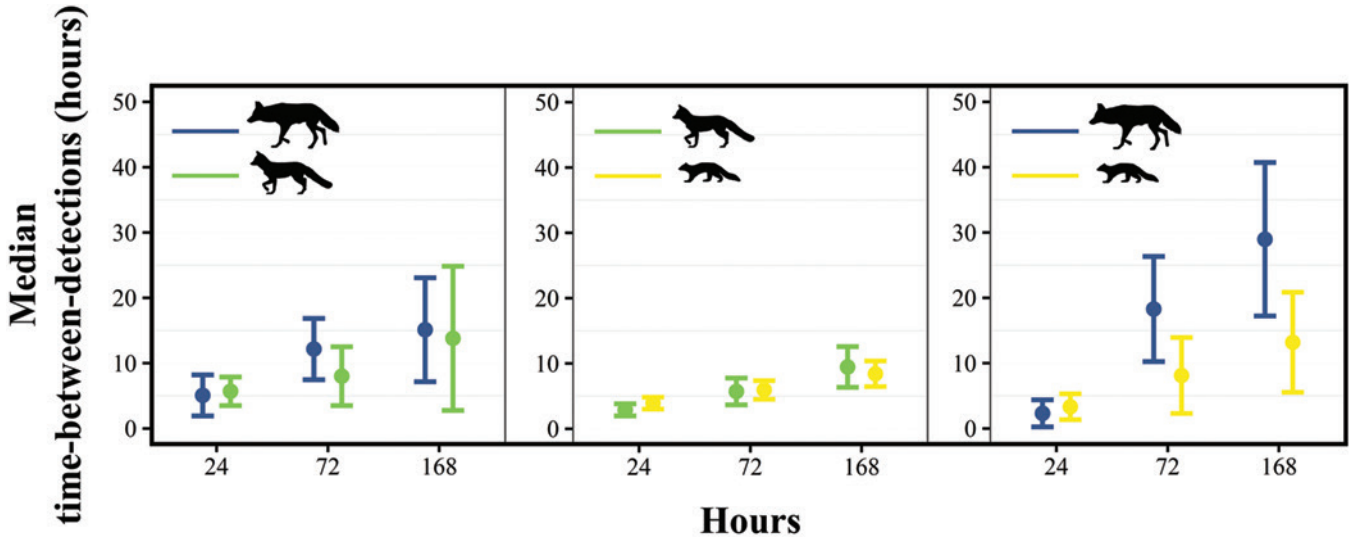

Fig. 8.—Median time-between-detections (±1.58 × IQR/√*n*) were computed from winter surveys (1 November to 30 April) deployed during the winters of 2014–2015 through 2016–2017 in the Greater Yellowstone Ecosystem, Wyoming. We defined time-between-detections as the difference in time of a focal species (e.g., Rocky Mountain Red Fox, *Vulpes vulpes macroura* = t_0) followed by a subsequent focal species (e.g., Pacific Marten, *Martes caurina* = t_1) at a single camera site. The time between the detection was calculated in hours (i.e., $t_1 - t_0$) in both directions for sequences of Pacific Marten, Rocky Mountain Red Fox, and Coyote (*Canis latrans*). The median time-between-detection was measured at 24-, 72-, and 168-h scales. The darker lines indicate the species that was first detected, followed by the other species within the figure. For example, in the left figure, the darker line illustrates that the Coyote was first detected and followed by a Red Fox. The lighter line illustrates that the Red Fox was first detected, followed by a Coyote. IQR is the interquartile range.

with coyote core home ranges, with foxes occupying rugged, high-elevation areas and coyotes occupying low-elevation areas (Fuhrmann 1998; Crabtree and Sheldon 1999). Similar elevational stratification has been documented between red foxes and coyotes in the Sierra Nevada mountains and the forested landscapes of Maine (Perrine 2005; Fuller and Harrison 2006). In our study, however, there was clearly elevational overlap in the mountains of the GYE, with coyotes occupying rugged, high-elevation areas (Table 1) and being detected at the same cameras as red foxes throughout the winter. Interference competition by coyotes may occur, particularly in later winter with resource limitations, but it remains unclear how detrimental it is to red foxes.

Before our study, coyotes were reported to be rare, if present at all, above 2,100 m in Yellowstone National Park (Fuhrmann 1998). In early winter, we detected coyotes above 2,100 m at 24 cameras with 1,228 photos. In late winter, we detected coyotes above 2,100 m at 54 cameras with 8,030 photos. The presence of coyotes in higher altitudes and mountainous terrain may be motivated by wolf avoidance. Subordinate mountain lions (Elbroch and Kusler 2018) in the GYE avoided wolves by selecting home ranges farther from known packs (Lendrum et al. 2014; Elbroch et al. 2015). During winter in the GYE, wolves often move to lower elevations alongside Elk (*Cervus canadensis*), their primary prey (Nelson et al. 2012). For instance, in our study, wolves were only detected 138 times at six cameras. These observations support the findings of Nelson et al. (2012) that wolves are likely absent in higher elevations during the winter in pursuit of elk, which may have implications on the distribution of some coyotes that choose to remain in the higher elevations where wolf density is lower.

Prey–predator insights.—Martens had significant differences in activity overlap between early and late winter with red squirrels and snowshoe hares (Figs. 5 and 6). Marten activity patterns stayed cathemeral across the winter season, with the only change being a slight increase in activity from dusk until midnight. We expected consistent activity from martens because they are the only predator we sampled that can easily access the subnivean zone, which should buffer them from resource constraints of late winter that their supranivean counterparts experience. Martens are behaviorally plastic in their diel activity patterns (Buskirk and Ruggiero 1994). Across the world, martens have displayed cathemeral activity throughout the year and winter (Foresman and Pearson 1999; Ikeda et al. 2016), diurnal activity in winter and crepuscular activity in summer (More 1978), or nocturnal activity (Marshall 1942; Roy et al. 2019). Martens appear to adjust their behavior for many reasons, including energetic demands and requirements and avoiding mortality (Drew and Bissonette 1997). Martens do not appear to change activity to avoid larger predators such as red foxes and coyotes, which both exhibit distinct peaks in activity (Fig. 7). Indeed, martens may be synchronizing activity with multiple prey species rather than avoiding larger predators (Zielinski et al. 1983; Ikeda et al. 2016). Martens are generalist predators (Buskirk and Ruggiero 1994), and cathemeral activity maximizes contact with many prey species on the snow surface and in the subnivean zone (Zielinski et al. 1983; Sherburne and Bissonette 1994; Buskirk 1999).

Red foxes exhibited differences in activity overlap between early and late winters with red squirrels and snowshoe hares (Figs. 5 and 6). Red foxes consistently displayed nocturnal and crepuscular activity across the winter season (Aubry 1983;

Voigt 1987; Perrine 2005), which was divergent from red squirrel activity but convergent with snowshoe hares. Overlap in Red Fox and Snowshoe Hare activity was high ($\Delta = 0.75$ in early winter, $\Delta = 0.70$ in late winter), consistent with snowshoe hares functioning as an important prey species for red foxes. Mountain red foxes in the Rocky Mountains and the Cascade Range rely upon snowshoe hares during the winter (Aubry 1983; Cross and Crabtree 2021). Despite the convergence of Red Fox and Snowshoe Hare activity, we observed a reduction in overlap between these two species in late winter, which may indicate a shift in red fox diet with increased consumption of ungulate carrion. In Interior Alaska, Sivy et al. (2018) found that when resource (e.g., voles and hares) availability was low in winter, red foxes consumed more carrion. With access to live and mobile prey such as voles decreasing in late winter associated with snow accumulation, the reduction in overlap between Red Fox and Snowshoe Hare activity may indicate a slight shift to carrion (Carricondo-Sanchez et al. 2016; Sivy et al. 2018; Gomo et al. 2021). In late winter and in high elevations, carrion is a stationary and subnivean resource, but it can still be accessed via digging by supranivean predators such as red foxes. Further work is needed to understand Red Fox diets during winter, and how that may underpin variation in temporal activity.

Of the three carnivores, coyotes were the only species that increased activity overlap with both red squirrels and snowshoe hares in late winter. The most noticeable change in activity occurred in late winter, with a predominant peak coinciding with Red Squirrel activity, and a corresponding increase with hares at dusk with continued activity through the night hours (Figs. 5 and 6). Coyotes exhibit primarily nocturnal and crepuscular activity, with some diurnal activity (Witmer and DeCalesta 1986; Bekoff and Gese 2003; Perrine 2005; Clevenger et al. 2013; Chitwood et al. 2020). Our results indicated nearly cathemeral activity in both early and late winter. We presume the cathemeral activity was related to food diversity and availability, including red squirrels and snowshoe hares as well as other prey, including rodents (murids and sciurids), and Grouse (*Bonasa umbellus*, *Dendragapus obscurus*; Crabtree and Sheldon 1999; Arjo et al. 2002; Dowd and Gese 2012; Sivy et al. 2017). The adaptability and plasticity in the winter diet of coyotes may be the primary means generating the cathemeral activity we observed in the mountains of the GYE.

Time-between-detections.—Our study expanded the use of camera data to evaluate interactions between forest carnivores at a finer scale than diel activity patterns. Our results indicated no significant differences in time-between-detections in each pair of species at all temporal scales (168, 72, and 24 h). Klauder et al. (2021) investigated the gap time between different scavenging species at the same ungulate carcass, and concluded that there was no significant pattern across 17 species pairs regardless of whether the first or second carnivore was larger or smaller in body size. Conversely, Prat-Guitart et al. (2020) used the time-between-detection approach to suggest that Florida panthers were more likely to move through an area after a prey species versus a competitor, and found that panthers did not temporally avoid any species examined. Although fine-scale time-between-detections have been effective for some studies (Prat-Guitart et al. 2020), the spatiotemporal scale of direct interactions, or interactions through olfactory or visual cues, may be too variable to detect consistent patterns via cameras. Global positioning system collars on multiple species (e.g., predator–prey and predator–predator) or paired scent, auditory, and camera stations may be a more effective means to assess questions directed at species interactions at a specific location (Eriksen et al. 2011; Basille et al. 2013; Brunet et al. 2022).

Conclusions.—We assessed activity patterns of three carnivores during winter within a mountainous and forested environment and used cameras to evaluate questions across multiple temporal resolutions. Our findings indicated that the activity of Pacific martens and Rocky Mountain red foxes remained similar between early and late winter, but coyotes displayed a comparatively large shift. The motivation underlying the shift in Coyote activity between early and late winter remains unclear. Still, it could be associated with coyotes aligning their activity with the activity of red squirrels and snowshoe hares, as well as other prey types, to increase the probability of encountering prey. The increase in prey overlap by coyotes, coupled with snow accumulation and relative stability in activity by red foxes and increased activity overlap between foxes and coyotes, potentially facilitates increased competition between foxes and coyotes in late winter. Our work indicated that time-between-detections at cameras might be too coarse and variable to assess the consequences of direct interactions between species. Others (e.g., Prat-Guitart et al. 2020) have generated insights related to species interactions using similar approaches—thus, additional work is needed to assess the strengths and weaknesses of applying cameras to evaluate fine-scale questions such as those in this study. Ideally, GPS collars, direct observation, and diet analysis would be coupled to further advance our understanding of spatiotemporal and dietary relationships between the suites of predators within our sampled ecosystem (e.g., red foxes, coyotes, mountain lions, wolves). This work could also be extended to summer, which would include two additional apex carnivores in black bears and grizzly bears (*U. arctos*), to address spatiotemporal and dietary relationships across the full suite of predators during a season of resource abundance. Our work supports the prediction that variation in time is an important axis in facilitating coexistence. Each species we sampled exhibited different activity patterns throughout the diel period, which may be a primary mechanism by which these species coexist in the mountains of the GYE.

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