



Activity of fishers at multiple temporal scales

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Ecologically relevant multi-temporal-scale frameworks elucidate whether patterns of animal activity (movement) are distinct at different temporal scales. We studied fishers (*Pekania pennanti*) fitted with transmitter collars that measured activity at high temporal resolution during winter in Wisconsin. A multi-temporal-scale framework with two scales, day (number of activity bouts per 24 h) and decision (time spent exploring a small area), revealed that the best models of fisher activity were different at different temporal scales. At the day scale, the fishers that we studied increased activity when temperatures were warmer and increased activity more when it was windy and cold than when it was windy and warm. At the decision scale, when wind speeds increased, female fishers reduced activity more than male fishers. The role of temperature on activity was only detected at the day scale, and intersexual variation was only detected at the decision scale. Results at both scales supported the prey synchrony hypothesis for activity, but support was mixed at the day scale. Assessing activity using a multi-temporal-scale analysis framework leads to a better understanding of factors that influence activity and biological fitness.

Key words: activity, fisher, multi-temporal-scale framework, *Pekania pennanti*, prey synchrony hypothesis, resource selection, temporal scale, Wisconsin

Resource selection is an inherently hierarchical process (Johnson 1980; Wiens 1989). Because of this, a more complete understanding of selection is acquired when analyses are conducted across multiple scales. When examining habitat selection, for example, researchers often examine multiple scales (Dumyahn et al. 2007; McCann and Moen 2011). Much as resource selection occurs in space, it also occurs in time when animals select different periods for activity (movement). Periods that influence biological fitness are resources (Schoener 1974) and different factors (independent variables) influence animal activity at different temporal scales that are hierarchically structured, ranging from macro (generations) to micro (minutes—Wolkovich et al. 2014). Studies of animal activity often focus on a subset of these temporal scales, including the day scale (e.g., number of activity bouts per 24 h—Zalewski 2000; McCann et al. 2017) and decision scale (e.g., time that elapses when exploring a small area—Podolski et al. 2013).

Multiple factors influence the timing of animal activity, including thermal conservation and prey availability. The

thermal conservation hypothesis postulates that animals select activity periods to increase energy conservation (Castillo et al. 2015). Reducing activity during cold and windy conditions, for example, increases thermal conservation (Porter and Gates 1969; Chappell 1980). The prey synchrony hypothesis postulates that synchronizing activity with the activity of prey increases capture rates for predators (Zielinski et al. 1983; Lode 1995), as active prey are more likely to be detected by predators (Fox 1969; Martel and Dill 2010; Ciuti et al. 2012). Thermal conservation and prey synchrony are likely to be linked, as prey that are less active during cold and windy conditions (for thermal conservation) are less likely to be detected by predators, which in turn should reduce activity to maximize hunting efficiency. Alternatively, predators may increase activity during these conditions to locate prey that are more difficult to detect, resulting in asynchrony.

Evidence suggests that our understanding of activity is sensitive to temporal scale. Activity of Eurasian lynxes (*Lynx lynx*), for example, corresponded with thermal conservation at the

day scale, but not at finer scales (Podolski et al. 2013). Activity of American martens (*Martes americana*) corresponded with mortality risk at the day scale, but not at finer scales (McCann et al. 2017). This suggests that analyses using multi-temporal-scale frameworks result in a more comprehensive understanding of how multiple mechanisms influence biological fitness because different factors influence activity at different temporal scales (McCann et al. 2017).

We used a multi-temporal-scale framework to investigate the winter activity of fishers (*Pekania pennanti*), a sexually dimorphic (males larger than females) boreal and subboreal forest carnivore that is relatively insensitive to cold winter temperatures (lower critical temperature of -20°C for females and -30°C for males—Powell 1979; Powell et al. 2003). Previous studies examined influences of environmental factors and sex on fisher activity during winter. The encounter rate of fisher tracks along transects was lower when temperatures were colder (Leonard 1980), but no changes were detected when it was windy (Leonard 1980). Fisher activity was lower during winter when compared with summer (Arthur and Krohn 1991), but intersexual variation in winter activity has not been found (Arthur and Krohn 1991; Weir and Corbould 2007). Although multiple studies examined fisher activity, we did not find any study that assessed fisher activity across multiple temporal scales. We hypothesized that both sexes of fisher would increase activity when ambient temperatures were warm and when winds were calm to synchronize activity with the activity of their prey. We also hypothesized that different factors would correspond with activity at different temporal scales, thereby elucidating scale-specific patterns of behavior.

MATERIALS AND METHODS

Study area.—We studied fishers on and near the Great Divide District of the Chequamegon-Nicolet National Forest in northern Wisconsin, United States (described by McCann et al. 2014). The region has cold and long winters. In January, the mean temperature was -12°C and mean precipitation was 19 mm (National Oceanic and Atmospheric Administration 2018).

The study area was in northern mesic forests containing sugar maple (*Acer saccharum*) and aspen (*Populus tremuloides*—Epstein et al. 2002). Sugar maple stands frequently included yellow birch (*Betula alleghaniensis*) and basswood (*Tilia americana*). White cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), red maple (*A. rubrum*), and black ash (*Fraxinus nigra*) occurred in lowlands. Hardwood understories often included patches of balsam fir (*Abies balsamea*), and common shrubs were hazelnut (*Corylus spp.*) and alder (*Alnus spp.*).

Livetrapping and handling fishers.—We used box-traps (model 108; Tomahawk Live Trap Co., Hazelhurst, Wisconsin) to capture fishers between October and February in 2008–2009 and 2009–2010. We fitted each fisher with a transmitter collar containing an activity switch that modulated the pulse period of signals emitted by the collar, resulting in pulse periods

that ranged from 1,081 to 1,320 ms and which were negatively correlated with the number of times the activity switch moved during the previous 16 min (Gilbert et al. 2009; model 125; Telonics, Inc., Mesa, Arizona). Animal-attached sensors like those we used measure behavior at high temporal resolutions (Cozzi et al. 2012), resulting in data that are comparable to direct observation (Brown et al. 2013). The capture and handling procedures we used followed established use and care guidelines (Purdue Animal Care and Use Committee 07-032; Sikes et al. 2016).

Monitoring fisher activity.—We used activity stations to record activity of fishers (randomly selected from our pool of collared individuals) for 1- to 2-week periods from 29 December 2008 to 21 March 2009, and 12 December 2009 to 13 March 2010 (described by McCann et al. 2017). Sampling corresponded with the pre-breeding season. Breeding commences in mid- or late March (Leonard 1980; Douglas and Strickland 1987) and 100% of day-scale and 94% of decision-scale data were from before 14 March.

Activity stations combined a data-logging receiver (model TR5; Telonics, Inc.) with a five-element antenna elevated 3 m above the surface of the snow. An activity station was placed within 2 km of a focal fisher. The activity station recorded 20 pulse-period readings of activity during each 15-min period.

Classifying fisher activity data.—We converted pulse-period records to activity readings by classifying pulse periods $\leq 1,104$ ms as active and pulse periods $> 1,104$ ms as inactive. Active pulse periods corresponded with highly active American martens wearing transmitter collars containing the same activity switch, while inactive pulse periods corresponded with resting and sleeping martens (P. A. Zollner, pers. obs.). For each 15-min period in our data set, we considered a fisher to be active when $> 50\%$ of pulse-period records were active ($\leq 1,104$ ms) and to be inactive when $\leq 50\%$ of pulse-period records were active. The active classification corresponded with collared fishers that we observed while they were walking and bounding, while the inactivity classification corresponded with motionless collared fishers (N. P. McCann, pers. obs.).

Periods when data were not recorded for ≤ 2 h occurred in our data set (i.e., when a fisher was not detected by the monitoring station), but such data gaps were rare (96% of activity records were 15 min apart). Periods in our data set that were > 2 h initiated a new monitoring session. Most new monitoring sessions were initiated after long periods without data, after the focal fisher moved away from the monitoring station (mean period with missing data that initiated a new monitoring period was 328.2 h, $SD = 312.4$ h, minimum = 2.5 h, maximum = 940.7 h, $n = 17$ data gaps between consecutive monitoring periods for the same fisher).

Collecting environmental data.—We used environmental data (at the same 15-min resolution as activity data) to develop models of fisher activity. We placed a weather station (HOBO; Onset Computer Corporation, Pocasset, Massachusetts) on high ground < 20 m from the data-logging receiver and antenna. This weather station recorded temperature, wind speed, and wind gust speed (maximum speed).

Statistical models of fisher activity.—We modeled fisher activity at each of two temporal scales: day and decision scales (McCann et al. 2017). We modeled fisher activity in response to sex, time of day, ambient temperature, wind speed, and wind gust speed. We used two different metrics to model time of day, each of which accounts for the circularity of time: $\sin(\text{time})$ and $\cos(\text{time})$. Our analysis focused on the day and decision scales, as data constraints precluded meaningful analyses at broader scales such as season. Other studies found snowfall to be negatively (Leonard 1980) and positively (Weir and Corbould 2007) correlated with fisher activity, but snowfall data were too sparse in our data set for analysis and were thus excluded.

For activity analyses at the day scale, we used linear mixed-effects models (LMMs) fit by maximizing the log-likelihood (Pinheiro et al. 2015). We modeled the number of activity bouts (multiple, consecutive 15-min samples of activity that were separated by multiple, consecutive 15-min periods of inactivity) per calendar day as a function of independent variables averaged across the same period (e.g., mean wind speed for the same day—Zalewski 2000; McCann et al. 2017). Decision-scale analyses used generalized estimating equations (GEEs) with a logit link function (Højsgaard et al. 2006) to model activity in response to independent variables, in which activity was scored as 1 when a fisher was active and was scored as 0 when inactive. We grouped data by individual for LMMs and used a first-order autoregressive residual covariance structure (to account for temporal autocorrelation) for all models. Variables included in multi-term models were not collinear ($r < 0.63$).

We evaluated models using an information theoretic approach and biologically based models (Burnham et al. 2011). For each temporal scale, day and decision, we constructed univariate models, and two-term additive and interaction models that contained lower terms. Results from these models are most appropriately interpreted for the fishers that we sampled, as our sample size of fishers was likely too small to make statements about the population. Degrees of freedom and effective sample size are difficult to determine when observational units are sampled more than once (as was the case here) and it is more appropriate to interpret results for sampled individuals when models might be overfit (Fieberg and Johnson 2015). Our sample sizes for monitoring and activity periods, however, were adequate to test whether the individual fishers that we sampled showed differences in behavior related to temporal scale.

We used information criteria to select best-fitting, parsimonious models ($\Delta\text{AIC}_c < 2$ for LMMs and $\Delta\text{QIC} < 2$ for GEEs—Burnham et al. 2011). We overcame model-selection uncertainty for LMMs by using full-model averaging (Burnham et al. 2011; Bartoń 2015), which greatly reduces bias when the number of data points is similar in magnitude to the number of variables considered (Lukacs et al. 2010). We calculated parameter estimates and 85% confidence intervals (CIs), which align parameter evaluation criteria with model selection (Arnold 2010).

RESULTS

We collected 4,660 15-min samples of activity from eight fishers (2,813 from four female fishers; 1,847 from four male

fishers). Samples of activity were acquired during 25 monitoring periods (periods that contained multiple 15-min samples of activity; 15 female fisher periods, 10 male fisher periods—Supplementary Data SD1) that had a mean duration of 50 h ($SD = 29$). We recorded activity and inactivity during all hours of the 24-h period (Fig. 1). Activity of the female fishers that we studied occurred during a mean of 20% of each monitoring period ($SD = 6\%$, $n = 15$ monitoring periods) and activity of the male fishers that we studied occurred during a mean of 21% ($SD = 12\%$, $n = 10$ monitoring periods). Female fishers had a mean of 4.2 active bouts each day ($SD = 1.5$, $n = 11$ days) that were a mean of 1.4 h ($SD = 1.4$, $n = 107$ active bouts), while male fishers had 4.0 active bouts each day ($SD = 1.4$, $n = 4$ days) that were a mean of 1.2 h ($SD = 1.4$, $n = 71$ active bouts).

At the day scale, activity of the fishers was correlated with temperature and wind speed. The univariate model containing the covariate for temperature, and the interaction model with covariates for temperature and wind speed each yielded $\Delta\text{AIC}_c < 2$ (Table 1). Parameter estimates for temperature and the interaction between temperature and wind speed were positive, each with CIs > 0 (Table 2). The fishers we studied had more active bouts on warm days (Fig. 2A) and the difference between the number of activity bouts at higher wind speeds (compared to lower wind speeds) was greater when it was cold than when it was warm (Fig. 2B). The number of bouts at -20°C , for example, was 1.5 times greater at 0.9 km/h than at 0.0 km/h but was only 1.2 times higher at 5°C (Fig. 2C).

At the decision scale, activity of fishers differed between the sexes and was correlated with wind speed. The model containing

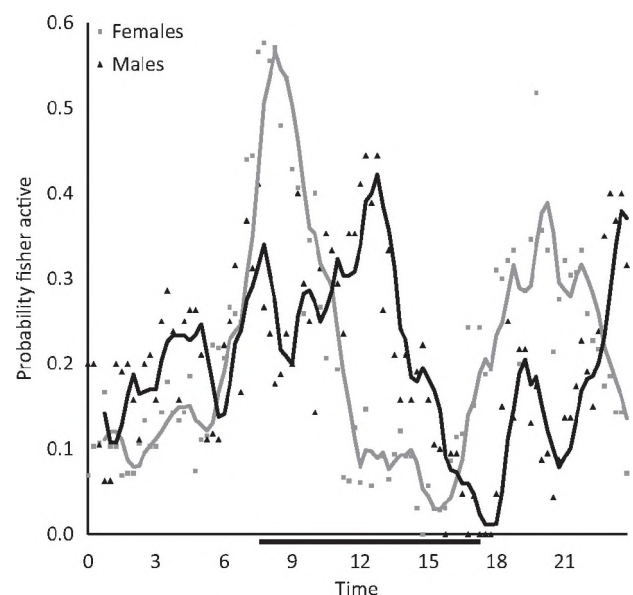


Fig. 1.—Probability of activity across the 24-h period for the female and male fishers (*Pekania pennanti*) that we studied during winter in northern Wisconsin, United States. Points represent 15-min probability estimates and lines (gray for female fishers, black for male fishers) depict the 1-h running mean probability. The black bar below the x-axis demarcates the mean period between sunrise and sunset during the study.

Table 1.—Day-scale fit statistics for models of winter activity for fishers (*Pekania pennanti*) in northern Wisconsin, United States. Akaike's Information Criterion (adjusted for small sample size; AIC_c) for the best model was subtracted from AIC_c for remaining models, resulting in ΔAIC_c for each model. Cumulative weight is the summed weight of the corresponding model and models with higher ranks.

Model	ΔAIC_c	Likelihood	Log(likelihood)	Cumulative weight
Temperature	0.00	1.00	−20.52	0.37
Temperature × wind speed ^a	0.79	0.68	−18.91	0.62
Sex ^b × temperature	2.20	0.33	−19.62	0.74
Wind speed	2.40	0.30	−21.72	0.85
Wind gust speed	3.26	0.20	−22.15	0.92
Sex × wind speed	3.80	0.15	−20.42	0.97
Sex × wind gust speed	5.34	0.07	−21.19	1.00

^aInteraction model contained lower terms.

^bFemales scored as 0 and males scored as 1.

Table 2.—Estimates with associated standard errors (*SEs*) and confidence limits (*CLs*) for parameters in fisher (*Pekania pennanti*) activity models from winter in northern Wisconsin, United States. We present parameters from models with information criterion values < 2 units from the top model at the day scale (see Table 1) and the decision scale (see Table 3). We averaged day-scale parameter estimates across the entire candidate set. Cumulative weight is the summed weight of the corresponding model and models with higher ranks.

Scale/parameter	β	<i>SE</i>	Lower 85% <i>CL</i>	Upper 85% <i>CL</i>
Day				
Temperature	0.15	0.04	0.10	0.20
Wind speed	1.56	0.48	0.89	2.25
Decision				
Sex ^a × wind speed ^b	0.18	0.09	0.06	0.31

^aFemales scored as 0 and males scored as 1.

^bInteraction model contained lower terms.

the interaction between sex and wind speed was the only model that yielded $\Delta QIC < 2$ (Table 3; Supplementary Data SD2). The parameter estimate for this interaction was positive and its *CI* was > 0 (Table 2). The probability of activity for female fishers was higher when wind speeds were lower (Fig. 3A). The probability of activity by male fishers was also higher when wind speeds were lower, but the difference in probabilities was less (Fig. 3B). The probability of activity by female fishers, for example, was 9.4 times greater at 0 km/h than at 10 km/h, whereas activity for male fishers was only 1.5 times greater at 0 km/h than at 10 km/h (Fig. 3A and 3B).

DISCUSSION

Examining influences of temporal scale is essential for understanding system dynamics (Morris 2003; Garnier et al. 2017). Studies of activity are common due to their importance for understanding animal behavior (Daan and Aschoff 1982; Eriksen et al. 2011). Investigations using multi-temporal-scale frameworks expose how different factors influence animal activity at different temporal scales (McCann et al. 2017). Our findings show that the activity of fishers that we monitored was correlated with different factors at the day and decision scales.

By using a multi-temporal-scale analysis framework, we found the activity of fishers was correlated with temperature and wind speed at the day scale, but activity differed between

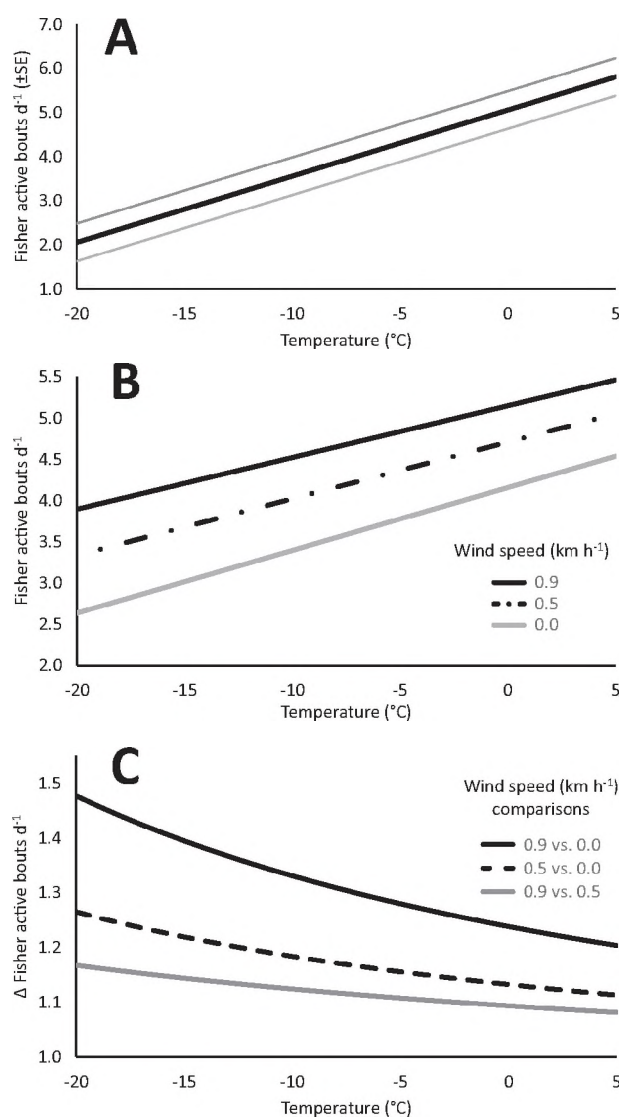


Fig. 2.—Relationship between the mean number of daily activity bouts (square-root-transformed) and temperature (A) and activity bouts and temperature and wind speed (B) for the fishers (*Pekania pennanti*) that we studied during winter in northern Wisconsin, United States. Panel (C) shows the difference (Δ) in activity bouts at two wind speeds while controlling for temperature across the range of temperatures we recorded, where Δ is the expected number of bouts at the higher wind speed divided by the number of bouts at the lower wind speed.

Table 3.—Decision-scale fit statistics for models of fisher (*Pekania pennanti*) activity during winter in northern Wisconsin, United States. Quasi-likelihood under the independence model criterion (QIC) for the best model was subtracted from QIC for remaining models, resulting in Δ QIC for each model. Only the 10 best models are shown. Cumulative weight is the summed weight of the corresponding model and models with higher ranks. Additional data are in [Supplementary Data SD2](#).

Model	Δ QIC	Log(quasi-likelihood)	Cumulative weight
Sex ^a × wind speed ^b	0.00	−2282.16	0.81
Wind speed	3.40	−2287.29	0.96
Wind speed + cosine(hour)	7.51	−2286.84	0.98
Cosine(hour) × wind speed	8.65	−2286.69	0.99
Wind speed + sine(hour)	10.11	−2285.59	1.00
Sine(hour) × wind speed	12.61	−2287.48	1.00
Wind gust speed	14.18	−2293.38	1.00
Cosine(hour)	17.05	−2293.04	1.00
Wind speed + sex	17.97	−2286.94	1.00
Wind gust speed + cosine(hour)	18.52	−2292.94	1.00

^aFemales scored as 0 and males scored as 1.

^bInteraction models contained lower terms.

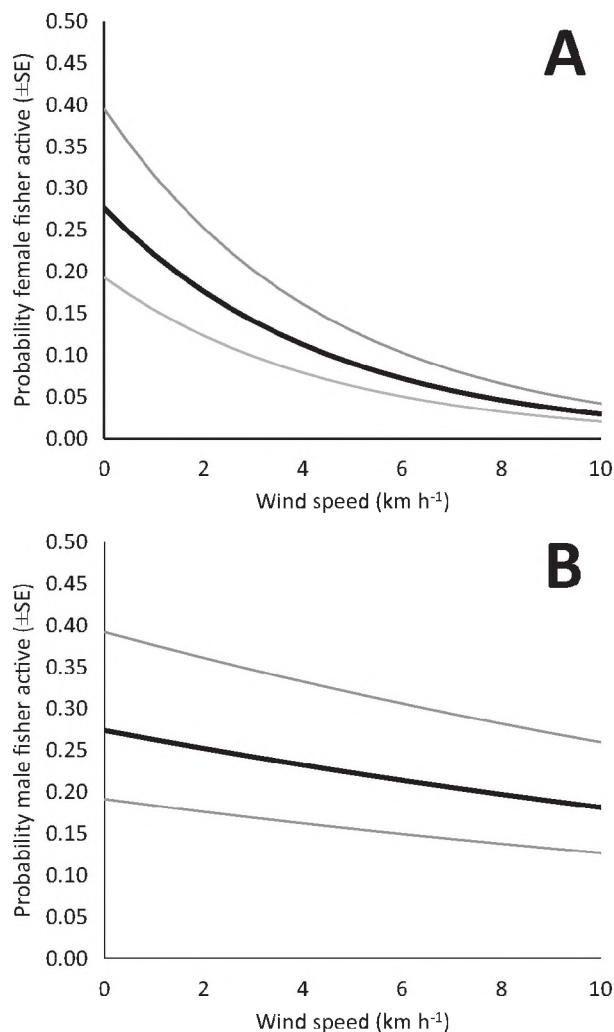


Fig. 3.—Relationship between the probability of activity for female fishers (*Pekania pennanti*) (A) and male fishers (B) and wind speeds measured at the decision scale during winter in northern Wisconsin, United States.

the sexes and was related to wind speed at the decision scale. Analysis at only the day scale would not have detected the effect of sex on activity. Analysis at only the decision scale would not have detected the correlation with temperature.

The positive relationship between activity and temperature supports the prey synchrony hypothesis for animal activity at the day scale. The activity of prey correlates positively with temperature (Lode 1995) and active prey are more likely to be detected by predators (Fox 1969). Increased activity of the fishers that we studied during warmer temperatures would have led to more time hunting when prey were easier to locate. This finding complements the finding of increased diurnal activity by fishers when it was warmer during snow-free periods (Weir and Corbould 2007), suggesting prey synchrony occurs throughout the year.

The positive relationship between activity of the fishers and temperature at the day scale is less likely to be explained by a need to reduce heat loss as ambient temperatures were almost always above the lower critical temperature for fishers. More than 94% of fisher activity was recorded when temperatures were greater than lower critical temperature for female fishers and 99.8% was recorded when temperatures were greater than the lower critical temperature for male fishers (Powell 1979).

The greater activity of the fishers when temperatures were cold and wind speeds were high (as compared to when it was cold and wind speeds were low) does not support prey synchrony at the day scale. Wind increases heat loss due to increased convection (Porter and Gates 1969; Chappell 1980). Fisher prey that are active during winter above ground would be exposed to cold temperatures and wind. Reducing activity during cold and windy conditions would increase thermal conservation for prey (Porter and Gates 1969; Chappell 1980). Reducing activity would also reduce detection by predators (Fox 1969; Martel and Dill 2010). This suggests that fishers increased activity during cold and windy conditions because it took more time for them to capture prey that were more difficult to detect, resulting in asynchrony with the activity of prey.

Intersexual variation in diet might explain why female fishers reduced activity at low wind speeds, while male fishers did not at the decision scale. Female fishers eat small prey more frequently (Weir 1995; Gilbert 2000) and larger prey (e.g., snowshoe hares, *Lepus americanus*—Gilbert 2000) less frequently than do male fishers (though differences are not always significant statistically—Leonard 1980; Giuliano et al. 1989). Smaller animals incur greater heat loss due to convection than do larger animals (Porter and Gates 1969; Chappell 1980). Hunting efficiency would have been reduced more for female fishers during windy conditions than for male fishers if smaller prey reduced activity during windy conditions to conserve energy, but larger prey did not. This is because active prey are more likely to be detected by predators (Martel and Dill 2010; Ciuti et al. 2012).

Our results complement findings from a study of American martens, in which sex, temperature, and wind speed influenced activity, and different factors influenced activity at different temporal scales (McCann et al. 2017). Although these results were similar to ours, other results differed. Time of day, for example, was an influential factor for martens but was not for fishers. Additionally, factors that were correlated with activity at one or more scales for martens were not correlated with activity for fishers. Temperature, for instance, was correlated with marten activity at the decision scale, but was not correlated with fisher activity at this scale. Collectively, these activity studies show that using multi-temporal-scale frameworks results in a more comprehensive understanding of behavior. They also show that patterns of activity differ between species, even for those with similar life histories.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Activity-monitoring periods for the fishers (*Pekania pennanti*) we studied in northern Wisconsin, United States, during winter.

Supplementary Data SD2.—Complete decision scale quasi-likelihood under the independence model criterion (QIC) table for models of fisher (*Pekania pennanti*) activity during winter in northern Wisconsin, United States. Cumulative weight is the summed weight of the corresponding model and models with higher ranks.

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