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FACTORS AFFECTING DIURNAL ACTIVITY OF FISHERS IN NORTH-CENTRAL BRITISH COLUMBIA

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Mustelids, with their long, thin bodies and poor fat storage capabilities, perform an energetic balancing act when making decisions about energy expenditure. Activity rates provide vital insights into the factors that may affect these energy balances. Using radiotelemetry, we examined factors that affected the likelihood of diurnal activity of fishers (*Martes pennanti*) in north-central British Columbia, Canada. We assessed the effect of 7 biotic and abiotic factors on the activity of 13 radiotagged fishers by considering 17 models using an information-theoretic approach. The best model suggested that, during the snow-free season, diurnal activity in fishers increased with increasing ambient temperature. The model also predicted that the activity of males increased during the mating season, compared to nonmating periods, whereas activity decreased during the mating season for females without young. Females with young were less likely to be active than females without young. Thus, factors that changed over both short and long terms affected the diurnal activity of fishers. Identifying these factors provides us with a better understanding of how rates of activity, and thus energy expenditure, change through time.

Key words: British Columbia, diurnal activity, fishers, *Martes pennanti*, radiotelemetry, reproduction, season, snow, temperature

Members of the family Mustelidae generally have long, thin bodies with high surface-to-volume ratios, which result in higher energetic costs for day-to-day life relative to many other mammals (Brown and Lasiewski 1972). Because of these morphometric characteristics, which also constrain energy storage, energy balances are very tenuous for these species (Harlow 1994). In addition, because many mustelids live in cold environments that pose further energetic challenges, rates of activity likely play an important role in their overall energy budget. American martens (*Martes americana*) are believed to constrain their activities when ambient temperature is below -15°C because of energy loss (Thompson and Colgan 1994), and their activity patterns may be a balance among thermal costs, exposure to predation risk, and prey vulnerability (Drew and Bissonette 1997). In the larger wolverine (*Gulo gulo*), searches for food and mating opportunities are believed to be the primary motivation affecting their activity (Banci 1994). Examining the activity patterns of fishers (*Martes pennanti*) provides us with an opportunity to evaluate the factors that may affect decisions regarding activity, and hence optimization of fitness, of a typical cold-environment mustelid.

Fishers exhibit a variety of complex behaviors in the acquisition of resources needed for their survival and reproduction (Powell 1993) and many factors have been reported to affect the timing and rates of their activity. Although initially believed to be primarily nocturnal (Coulter 1966; de Vos 1952), more recent studies have reported that fishers tend to be crepuscular (i.e., most active at sunrise and sunset—Arthur and Krohn 1991; Johnson 1984; Kelly 1977; Powell 1993). Periods of activity are generally 2–5 h long and often are separated by longer stretches (>10 h) of inactivity (Powell 1993).

Intrinsic factors have been reported to play an important role in the activity patterns of fishers. During spring, denning (i.e., parturient) female fishers are reported to be more active than nondenning females as expected, given energy demands for nursing (Arthur and Krohn 1991). Also, Arthur and Krohn (1991) and Kelly (1977) both reported that fishers were more active in summer than in winter. Male fishers also may be more active than female fishers (Kelly 1977), especially during the breeding season when they are attempting to locate mates (Arthur and Krohn 1991).

Extrinsic factors also may affect activity rates of fishers. Deep, soft snow can inhibit movement during winter and, because of this, fishers are reported to modify their small-scale movements to avoid areas with less-supportive snow (Leonard 1980, Raine 1983). Fishers also may modify their behavior during periods of extreme cold (Weir et al. 2004).

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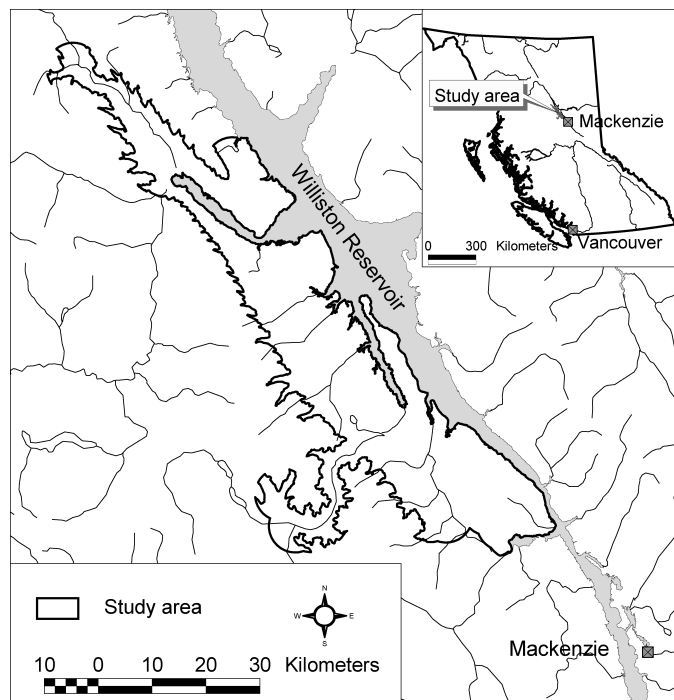


FIG. 1.—Location of study area in north-central British Columbia, Canada, 1996–2000.

Identifying the primary factors that affect activity patterns of fishers will provide us with insight into the limitations within which fishers expend energy and acquire resources. Understanding the basis of this relationship will help us to predict the effects of changes in the distribution and abundance of resources (e.g., alteration of habitat and effects of global warming) on the ability of the landscape to support fishers.

We expect activity rates of fishers to be affected by both extrinsic and intrinsic factors, as identified by previous researchers, including temporal proximity to twilight, season, abiotic factors (e.g., snow conditions and ambient temperature), reproductive status, and sex of the animal. In this study, we used radiotelemetry data collected from fishers in the subboreal forests of north-central British Columbia, Canada, to examine these hypotheses.

MATERIALS AND METHODS

The study area covered approximately 1,930 km² and was centered 70 km northwest of Mackenzie, British Columbia (55°30'N, 123°02'W; Fig. 1). The study area was composed of 2 subzones of the subboreal spruce biogeoclimatic zone. The moist, cool subzone of the subboreal spruce zone occurred at elevations below 800 m, whereas the wet, cool subzone occurred between 800 and 1,100 m (MacKinnon et al. 1990). The moist, cool subzone comprised 80% of the study area. Annual precipitation was 690 mm in the moist, cool subzone and 905 mm in the wet, cool subzone (MacKinnon et al. 1990). Snowfall was 335 cm/year in the moist, cool subzone and 1,075 cm/year in the wet, cool subzone (MacKinnon et al. 1990). Snow cover in the study area generally lasted from mid-

November until mid-April and reached an average peak snow depth of 0.77 m ($SD = 0.29$ m, $n = 4$) during the study. Mean annual temperature during the study was 2°C and daily temperature ranged between -47°C and 36°C.

Forests in the moist, cool subzone were dominated by hybrid spruce (*Picea glauca* × *engelmannii*), lodgepole pine (*Pinus contorta*), black spruce (*Picea mariana*), and subalpine fir (*Abies lasiocarpa*), with deciduous components of trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Black cottonwoods (*Populus balsamifera trichocarpa*) occurred as a minor element in riparian ecosystems and occasionally in other areas with subhygric or wetter ecological moisture regimes. The composition of forests in the wet, cool subzone was similar, with hybrid spruce and subalpine fir being more dominant. Common understory shrubs in both subzones were prickly rose (*Rosa acicularis*), black huckleberry (*Vaccinium membranaceum*), black twinberry (*Lonicera involucrata*), kinnikinnick (*Arctostaphylos uva-ursi*), and black gooseberry (*Ribes lacustre*).

The moist, cool subzone typically had a natural disturbance regime of frequent, large-scale fires with a mean return interval of about 127 years, whereas the wet, cool subzone had a mean fire return interval of 270 years (DeLong 1998). Forest harvesting, using a variety of techniques, had occurred over the past 25 years and resulted in a mosaic of seral stages and stand types throughout the study area.

We live-captured and radiotagged fishers throughout the study area between 1996 and 2000. Fishers were immobilized using a 10:1 mixture of ketamine hydrochloride: xylazine hydrochloride, a 5:1 mixture of ketamine hydrochloride: medetomidine hydrochloride, or a 1:1 mixture of tiletamine hydrochloride: zolazepam hydrochloride. We used 2 methods to radiotag fishers. During the first 2 years of the study, we tagged fishers with external radiocollars (M-2; Holohil Systems Ltd., Carp, Ontario, Canada; MOD-080; Telonics Inc., Mesa, Arizona). In subsequent years, we tagged the fishers with intraperitoneal implant transmitters (IMP/200/L or IMP/300/L; Telonics Inc.), which involved surgery conducted by a veterinarian under aseptic conditions in the field. All capture, handling, and tagging protocols followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and met standard levels of animal care that were equivalent to those recognized by the Canadian Council on Animal Care.

We estimated the activity of free-ranging radiotagged fishers based on the strength and consistency of their respective radiosignals from ground telemetry (Arthur and Krohn 1991; Drew and Bissonette 1997). Radiosignals from resting fishers were usually strong and consistent, whereas fishers that were active usually produced signals that fluctuated greatly in both strength and consistency. We classified each radiolocation as “active,” “not active,” or “unknown.” “Not active” radiolocations were those where the signal was strong, the strength did not fluctuate noticeably, and the transmitter location did not change within the monitoring period. “Active” radiolocations were those where the signal fluctuated greatly and the transmitter location changed during monitoring. “Unknown” occurred when the radiosignal was neither clearly constant nor fluctuating.

TABLE 1.—Candidate models used to examine factors that affected the likelihood of diurnal activity of radiotagged fishers (*Martes pennanti*) in the Williston region of north-central British Columbia, Canada, 1996–2000. An asterisk (*) demarks 95% confidence set of best models. $n = 368$ radiolocations of 13 fishers.

Model description	K^a	QIC_u^b	Δ_i^c	w_i^d
* T_a^e during the snow-free season, reproductive condition depending upon sex	5	457.8	0	0.451
* Presence of ≥ 5 cm new snow during winter, T_a during the snow-free season, reproductive condition depending on sex ^f	6	458.4	0.6	0.326
* Total snow depth during winter, T_a during the snow-free season, reproductive condition depending on sex	6	459.7	1.9	0.175
New snow depth during winter, proximity to twilight during the snow-free season, reproductive condition depending on sex	5	463.7	5.9	0.023
New snow during winter, T_a during winter, proximity to twilight	6	464.5	6.7	0.016
Global model	10	465.6	7.8	0.009
T_a during winter, proximity to twilight, reproductive condition depending on sex	5	478.0	20.2	<0.001
Reproductive condition (Arthur and Krohn 1991)	3	486.6	28.8	<0.001
Reproductive condition depending on sex	4	487.4	29.7	<0.001
Snow depth during winter, T_a during the snow-free season	3	487.9	30.1	<0.001
T_a during the snow-free season	2	490.0	32.2	<0.001
Proximity to twilight, season, sex (Kelly 1977)	4	499.3	41.5	<0.001
Season	2	502.6	44.8	<0.001
New snow, T_a (Leonard 1980; Raine 1983)	3	504.8	47.0	<0.001
Sex (Johnson 1984; Kelly 1977)	2	506.1	48.3	<0.001
Proximity to twilight (Arthur and Krohn 1991; Johnson 1984; Kelly 1977; Powell 1993)	2	507.5	49.7	<0.001
Null model	1	510.0	52.2	<0.001

^a K = number of estimated parameters in associated model.

^b QIC_u = quasiliikelihood information criterion (Pan 2001).

^c Δ_i = difference in QIC_u scores between model and best-selected model.

^d w_i = Akaike weight (Burnham and Anderson 1998).

^e T_a = ambient temperature ($^{\circ}\text{C}$).

^f See “Materials and Methods” for definition of reproductive condition depending on sex.

We did not observe substantial differences in the characteristics of signal attenuation between collar and implant transmitters.

We attempted to collect 4–8 radiolocations per fisher for each month during our monitoring periods. For each radiolocation, we collected data on temporal proximity to twilight (i.e., hours from sunrise or sunset), season (winter [16 November–15 April] or snow-free [16 April–15 November]), concurrent local ambient temperature, snow conditions (total depth of snow and depth of new snow in past 24 h), reproductive condition, and sex of the individual.

Temperature and snow data were recorded at 5 climate stations throughout the study area. Climate stations were placed at flat sites under typical forest canopy at least 10 m from the forest edge in well-ventilated shaded locations approximately 2 m above ground level. We recorded daily maximum and minimum temperatures, total snow depth, and total fresh snowfall during the previous 24 h at the stations. We added remote temperature data loggers (Optic Stowaway; Onset Computer Corp., Bourne, Massachusetts) to record hourly temperatures at all climate stations from October 1998 onward. In late 1998, we also began to collect climatic data using a single remote snow-monitoring station (Campbell Scientific, Edmonton, Alberta, Canada) containing sensors to measure ambient temperature (2 m above ground level) and snow depth every 2 h.

We classified the timing of reproductive behavior differently among age and reproductive classes. We classified radiolocations from female fishers with young as being from the rearing period if they occurred from 2 days before the observed whelping date to 30 June. For males, we considered radio-

locations to be from the mating period if they occurred between 1 March and 15 May (Powell 1993). We considered radiolocations from females without young to be from the mating period if they were collected between 1 April and 15 May. All other radiolocations were considered to be from the non-reproductive period.

We assessed the effect of temporal proximity to twilight, season, total snow depth, presence of ≥ 5 cm of snow fallen during past 24 h, ambient temperature, reproductive status, and sex on the likelihood of activity of fishers by considering these factors in several competing models using an information-theoretic approach (Burnham and Anderson 1998). Essentially, information-theoretic inference allows us to compare the support, by the data, among several hypothetical models and determine the probability of each model in the candidate set being closest to “reality.” We used information from previous studies of fisher ecology and suspected ecological relationships to develop 17 a priori models that we tested. We examined the support by the data for each of the models composed of arrangements of these variables, with the global model including all 7 variables (Table 1). We considered activity as a binary response variable (i.e., active or not active) and used logistic regression methods to parameterize each of the models. We assessed multicollinearity among variables with ordinary least-squares regression. In cases with correlation coefficients ≥ 0.4 , we excluded 1 set of the correlated variables from the model on the basis of a priori knowledge. We included only those radiolocations where the fisher was classified as active or not active in our analyses.

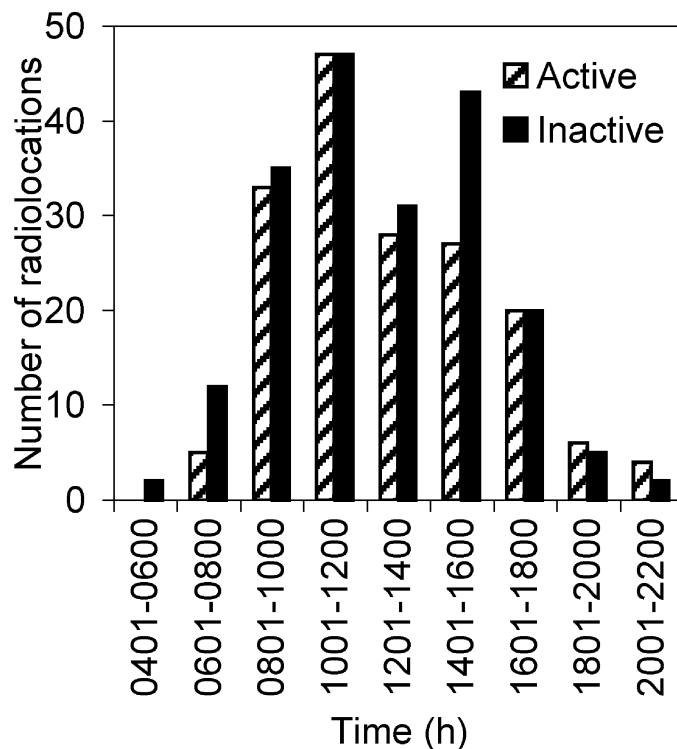


FIG. 2.—Effect of time of day on activity of radiotagged fishers (*Martes pennanti*) in north-central British Columbia, Canada, 1996–2000. Cross-hatched bars represent radiolocations during which the fisher was active, whereas the solid bars represent inactive fishers; $n = 368$ radiolocations.

Because we collected multiple observations from a fixed number of fishers, we expected that data points would not be independent. To account for the longitudinality of these data, we employed generalized estimating equations to derive a population-averaged model (Hosmer and Lemeshow 2000: 311), which predicted the proportion of radiolocations when fishers were active.

We used an information-theoretic approach (Burnham and Anderson 1998) to identify the most parsimonious model to predict activity among radiotagged fishers. However, because generalized estimating equations are not likelihood-based, we used a modification to the Akaike information criterion to produce a quasiliikelihood information criterion (QIC_u —Pan 2001). We assumed that correlation of data only occurred within individuals, which allowed us to select exchangeable correlation as our working correlation structure. We calculated the QIC_u score for each model and ranked the relative support for each by comparing this score among the competing models. We identified the best model from our candidate set by selecting the model with the lowest QIC_u score. We considered the best model to be definitive relative to other models in the candidate set if the Akaike weight (w_i —Burnham and Anderson 1998) was >0.95 . If the top model was not definitively the best, we included the top models in the 95% confidence set such that the sum of their Akaike weights was ≤ 0.95 .

We used multimodel inference (Burnham and Anderson 1998) to estimate model-averaged parameters and unconditional 95% confidence intervals for each of the variables in the production of a best predictive model. We used the odds ratios for each variable found in the best models to predict how the probability of diurnal activity would change with increasing or decreasing values of each variable.

RESULTS

We collected 368 radiolocations of 13 fishers (10 females and 3 males) between 7 December 1996 and 18 July 2000 that we could classify as either active or not active ($\bar{X} = 28$ radiolocations/fisher ± 25 SD). We collected 134 radiolocations during the snow-free period and 234 during the winter period. We collected 293 radiolocations of females and 75 radiolocations of males that were suitable for inclusion in the analysis.

Fishers were active on 170 occasions (46%) and not active 198 times (54%). Males were active for 59% of their locations, whereas females were active for 43% of their locations. Fishers were active at 45% of radiolocations during the snow-free season and 47% during winter. Fishers were active throughout the diurnal period, with some minor peaks in activity around noon and early evening (Fig. 2).

The data had almost equal support for 2 models as being the best from our candidate set (Table 1). The model that explained diurnal activity as being affected by ambient temperature during the snow-free season and reproductive condition depending upon sex ranked 0.6 QIC_u units lower (i.e., better) than the 2nd-best model, which was a slightly expanded version of the best model. This 2nd-best model included 1 additional variable: presence of ≥ 5 cm of new snow during the past 24 h during winter. These 2 top models were almost equally supported by the data; the best model was only 38% more likely to be the actual best model than the 2nd-best model in the candidate set (Burnham and Anderson 1998). The 95% confidence set of models was rounded out with a 3rd model that included total snow depth during winter, ambient temperature during the snow-free season, and reproductive condition depending upon sex.

The multimodel parameterization of the top models (Table 2) suggested that the activity of fishers changed with several intrinsic and extrinsic factors. The parameterized best model suggested that the presence of ≥ 5 cm of new snow during winter increased the likelihood of activity by 85% and that an increase in ambient temperature during the snow-free season of 5°C increased the likelihood of activity by 55%. It also predicted that females with young were 300% less likely to be active than females without young. Examination of the data suggested that males during reproductive periods were more likely to be active than during nonreproductive periods and that mating females were less likely to be active than nonmating females; however, the 95% confidence intervals around the odds ratio for these variables encompassed 1, so we could not determine with confidence whether the effect of these variables was positive or negative.

DISCUSSION

Examination of our data suggested that factors that affected the likelihood of diurnal activity by radiotagged fishers were not necessarily those that fluctuated over short time scales, as had been documented in other studies of fishers (e.g., Johnson 1984; Kelly 1977). Rather, activity seemed to be related to extrinsic and intrinsic factors that changed over both long and short time periods. The important variables of reproductive condition changed over months, whereas ambient temperature and snowfalls varied daily.

Our observation that the likelihood of diurnal activity was affected by ambient temperature during the snow-free season has not been reported in the literature. Faccio (1992) did not detect any substantial effect of temperature on activity rates, although he did note that activity seemed to be related to concurrent cloud cover and precipitation values. From an energetic perspective, all of the ambient temperatures that we encountered during the snow-free season (range: -8.9°C to 29.4°C) were well above the lower critical temperature estimated for active fishers (-20°C for females and -30°C for males—Powell 1993) and thus, we did not expect a behavioral response to ambient temperature during this period.

Fishers may have increased their activity with ambient temperature because foraging opportunities were better at warmer temperatures during the snow-free season. The activity of prey may be greatest during warmer temperatures (red squirrels—Obbard 1987; snowshoe hares—Theau and Ferron 2001) and fishers may have synchronized periods of activity with their prey to increase the probability of successful foraging. Perhaps fishers keyed in on less wary juvenile prey items that were most vulnerable during warm temperatures of the snow-free season. It is unclear as to why the relationship between ambient temperature and diurnal activity was not evident during the winter period.

Diurnal activity also was affected by the reproductive status of the fishers. This factor was mediated by sex, which was not unexpected. Male fishers are expected to be more active during the breeding season while searching for mates (March–May—Arthur and Krohn 1991), which we observed. Contrary to our results, however, Arthur and Krohn (1991) and Leonard (1980) observed that female fishers with young were more active than females without young, presumably because females needed to spend more time foraging during this period. Yet, our observations that females with young spent much of their time during the reproductive period in their respective natal and maternal dens suggest that other factors affect their activity rate while rearing young. Perhaps females need to spend more time nursing their young or provide thermal or security protection, or prey was sufficiently abundant that they did not have to forage for extended periods of time to sequester adequate food. Alternatively, we collected more radiolocations on females with young during the 1st month after whelping than later during the rearing period (56 radiolocations during April, compared to 22 and 18 radiolocations in May and June, respectively). This may have weighted our observations to periods when females needed to spend more time with their young.

TABLE 2.—Parameterization of equivocal best models from candidate set to explain the factors affecting the likelihood of diurnal activity of radiotagged fishers (*Martes pennanti*) in the Williston region of north-central British Columbia, Canada, 1996–2000.

Parameter	Composite coefficient	Odds ratio	Unconditional 95% CI ^a	
			Lower	Upper
Intercept	−0.011	0.99	0.96	1.02
Presence of ≥ 5 cm new snow during winter ^b	0.614	1.85	1.00	3.42
T _a ^c during the snow-free season	0.088	1.09	1.03	1.15
Mating reproductive condition for males ^d	0.467	1.60	0.91	2.79
Mating reproductive condition for females ^d	−0.161	0.85	0.44	1.66
Rearing young ^d (females only)	−1.375	0.25	0.14	0.46

^a 95% CI = 95% confidence interval.

^b During previous 24-h period.

^c T_a = ambient temperature ($^{\circ}\text{C}$).

^d Compared to reference value of “nonreproductive.”

Our observation that the likelihood of activity of fishers increased with fresh snowfalls of ≥ 5 cm during winter is contrary to many other findings. Specifically, both Leonard (1980) and Raine (1983) observed that fishers reduced their movements during periods of deep snow. However, it is likely that the characteristics of the snow in our study area were substantially different than those found in the more continental boreal forest in which Leonard's (1980) and Raine's (1983) studies occurred. In our study area, snowfalls often were followed by thaws and subsequent freezing temperatures that produced snowpacks with numerous snow layers that had variable densities (R. D. Weir, in litt.). Once new snow settled during these thaw–freeze events, the base upon which new snow fell may have been substantially firmer than other areas. Thus, new snow may not be a substantial impediment to movement for fishers. Perhaps there is a predatory benefit to new snow or it is easier to capture small prey in soft snow. Conversely, fishers may have to move more widely, and thus spend longer periods being active, because prey is more difficult to locate. This relationship is counterintuitive and requires further examination.

The models in the candidate set that were least supported by our data were simple models that included 1 or 2 variables. The fishers that we had radiotagged did not appear to be consistently crepuscular, as reported by Johnson (1984) and Kelly (1977). Models that included proximity to twilight were not well supported by our data, although most radiolocations were collected during daylight hours, which may have biased our data. Models that were based on the simplistic categories of season or sex (Johnson 1984; Kelly 1977) also were least supported by our data. Instead, our analysis suggested that an array of factors affected the diurnal activity of fishers.

It is possible that the motivation behind the activity patterns that we observed was the result of other intrinsic factors affecting fishers, rather than the extrinsic abiotic or biotic factors that we measured. Factors such as time since last meal or hormone levels may more closely affect activity by fishers.

Also we did not examine, nor have data for, habitat-related factors or other spatial factors that may have affected the likelihood of activity of an individual, such as habitat quality or prey catchability.

Unfortunately, our data on activity rates were limited to diurnal time periods, primarily on the daytime side of twilight. It is possible that activity patterns during other portions of the circadian period are substantially different. Consequently, activities that occurred during our monitoring periods may have been influenced by activities that were primarily nocturnal. Unless activity rates are consistent between the nocturnal and diurnal periods, one period will undoubtedly have an influence on the other. Additional research is required to describe the nocturnal activity patterns of fishers, and thus provide a more complete understanding of their diel activity rates.

Conservation implications.—Because of their long, thin bodies and poor fat storage capabilities, energy balances for fishers are more critical for this species than others (Harlow 1994). Altering either the spatial or temporal factors that affect the ability of fishers to acquire resources may negatively affect energy balances. Consequently, human activities that affect the distribution and abundance of the resources required by fishers can ultimately affect the ability of individuals to occupy an area. Given a better understanding of the temporal factors that affect activity rates of fishers, we can better speculate on the effects of changes to the distribution and abundance of resources on the energy balance of this species.

Examination of our data provides a better understanding of the temporal patterns within which fishers acquire resources. Activity rates provide a glimpse into the day-to-day factors that affect decisions that fishers made regarding the allocation of time and resources. These budgets may constrain other facets of the ecology of fishers, such as responses to habitat change or population perturbation. Understanding the temporal patterns of activity also provides us with better conceptualization of behavioral patterns, such as foraging and movements.

Our findings that diurnal activity rates were related to both biotic and abiotic factors provides us with a framework through which we may be better able to predict changes to the energy balance of fishers in British Columbia. This is particularly important given the ongoing anthropogenic changes to the distribution and abundance of resources used by fishers. Understanding the factors that affect the decisions regarding energy expenditure by fishers also has implications for understanding energy budgets of other cold-environment mustelids, such as American martens.

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