



Poor body condition and diet diversity in a harvested population of fishers

Authors: Kirby, Rebecca, Freeh, Carissa, Gilbert, Jonathan H., Olson, John F., and Pauli, Jonathan N.

Source: Wildlife Biology, 2018(1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00334>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Poor body condition and diet diversity in a harvested population of fishers

Rebecca Kirby, Carissa Freeh, Jonathan H. Gilbert, John F. Olson and Jonathan N. Pauli

R. Kirby (<http://orcid.org/0000-0002-4016-2173>) (kirbyr@gmail.com), C. Freeh and J. N. Pauli, Dept of Forest and Wildlife Ecology, Univ. of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA. – J. H. Gilbert, Great Lakes Indian Fish and Wildlife Commission, Odanah, WI, USA. – J. F. Olson, Wisconsin Dept of Natural Resources, Ashland, WI, USA.

Though fishers *Pekania pennanti* were extirpated from most of their historical range in the United States, they have successfully repatriated many areas, and are now legally harvested in the Great Lakes region. Recent harvests and winter track surveys, however, suggest fisher populations may again be decreasing in northern Wisconsin. We investigated potential factors contributing to this purported decrease by quantifying fisher diet in northern Wisconsin via stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and examining body condition of individual fishers using measurements of fat depots. Diet reconstruction revealed small mammals and porcupines constitute the largest portions of fishers' diets in Wisconsin. Body condition analyses showed that contemporary fishers carry significantly less body fat compared to Wisconsin fishers two decades ago and to two other regional populations. Our findings contrast with past regional studies that report snowshoe hares and white-tailed deer carrion as the largest components of fisher diet. We suggest the diet and body condition of fishers in Wisconsin could be due to low availability of preferred prey other than porcupines on the landscape, which may be contributing to the recent putative population decrease.

Carnivorous populations have historically decreased globally due to overexploitation, persecution, and habitat loss (Ripple et al. 2014). Nonetheless, following legislative protections, improved logging practices, and active management some species have rebounded across Europe (Chapron et al. 2014) and North America (Linnell et al. 2001). In human-dominated landscapes, ecological generalists are more likely to recover and persist (Erwin 1998, McKinney and Lockwood 1999), while specialists are particularly vulnerable to extinction (Boyles and Storm 2007). The fisher *Pekania pennanti* is a forest specialist mesocarnivore associated with northern forests in North America (Powell et al. 2017). Following habitat loss and overexploitation in the 1800s, the range of fishers contracted considerably (Powell 1993). With trapping closures and reintroduction efforts, fisher populations recovered throughout many parts of their historical range in eastern and central North America (Lewis et al. 2012), possibly due, in part, to fishers' diet flexibility (LaPoint et al. 2015).

Although forest specialists, fishers have the flexibility to be dietary generalists, consuming small and mid-sized

mammals, birds, fruits and carrion (Powell 1993, Powell et al. 2017). Where their ranges overlap, snowshoe hares *Lepus americanus* are fishers' most common diet item (Powell and Zielinski 1994). Additionally, fishers possess the uncommon ability to prey efficiently on North American porcupines *Erethizon dorsatum* when available (Powell 1993, Pokallus and Pauli 2015). The availability of either of these important prey species can lead to stable fisher populations (Bulmer 1974, Bowman et al. 2006). Squirrels and small mammals appear to be used as important alternative prey when preferred prey are scarce (Kuehn 1989, Martin 1994, Bowman et al. 2006, Jensen et al. 2012). Prey consumption varies markedly across their range and fishers in the Great Lakes region generally consume more large-bodied prey than eastern or western populations (LaPoint et al. 2015).

American martens *Martes americana*, a close relative, can be sympatric with fishers and share many dietary items (Buskirk and Ruggiero 1994, Zielinski and Duncan 2004). Recent research suggests that martens in northern Wisconsin are consuming fewer optimal prey items, relying more on smaller prey like shrews, *Blarina brevicauda* and *Sorex* spp., as well as prey like deer carrion that is likely riskier due to competition with other predators (Carlson et al. 2014). This finding may be evidence that the small prey community in northern Wisconsin is changing, resulting in different prey availability and enhanced interspecific competition. Unlike martens, fishers exploit porcupines (Bowman et al. 2006). In

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <<http://creativecommons.org/licenses/by/4.0/>>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

fact, they are energetically more efficient when consuming larger-bodied prey (Powell 1979) and may, then, be more resilient to a declining small prey base with minimal effects on their body condition (Kuehn 1989, Helldin 1999) and survival. As active predators, fishers and other mustelids rely on adequate fat depots as an important energy source (Leonard 1980, Buskirk and Harlow 1989, Robitaille and Cobb 2003). Such fat depots are critical for survival and can be used as an index of nutritional condition reflecting rates of energy intake (DeCalesta et al. 1975, Schulte-Hostedde et al. 2005). The capacity to store adipose tissue varies widely within the weasel family – American martens are lean (2.4–5.6% body fat, Buskirk and Harlow 1989), whereas fishers can carry larger reserves (2–32% body fat, Garant and Cr te 1999). Across mustelids, within a species, a comparatively low percent body fat can indicate an animal is in poor condition (Mustonen et al. 2015). Fat dynamics can vary from a variety of factors including prey availability (Robitaille and Jensen 2005). For example, Kuehn (1989) found that the amount of fat in fishers from Minnesota increased as deer harvest levels increased, indicating the potential importance of carrion to fishers.

Although historically fishers were distributed across the Great Lakes region, extensive logging and high harvest pressure resulted in severe range contraction and fishers were extirpated in Wisconsin and Michigan by the 1930s (Williams et al. 2007, Lewis et al. 2012). Reintroductions in the 1950s, coupled with natural recolonization, resulted in the recovery of fishers to the region so that regulated harvests were again implemented in Michigan, Minnesota, and Wisconsin (Berg and Kuehn 1994, Williams et al. 2007, Lewis et al. 2012). Nevertheless, recent harvest and winter track survey data (2002–2013) suggest that the fisher population in northern Wisconsin is again decreasing (Rolley et al. 2013). Research has also documented a northward shift regionally of the southern boundary of snowshoe hares (Saultaire et al. 2016), as well as many small mammals associated with northern forests (Myers et al. 2009). We hypothesized that fishers have sub-optimal prey resources and we investigated limited energy intake as a possible mechanism of their population decrease. We quantified fisher diet in northern Wisconsin and contrasted individual body condition. We estimated diet components of the contemporary population via stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and compared body condition between contemporary, historical and regional populations of fishers via analysis of fat depots.

Material and methods

Sample collection

We obtained carcasses of fishers trapped during the 2013 trapping season, October–December, in Wisconsin. We collected hair samples ($n=47$) and omental fat depots ($n=54$) from fisher carcasses and froze them for subsequent analyses. We estimated age from cementum annuli (Matson's Lab, Milltown, MT, USA). During spring, fall, and summer seasons of 2010–2013 we collected potential food samples (hair, feathers and vegetation) in northern Wisconsin from small mammals that we live-trapped, from vegetation

surveys, and from deer carcasses. Because we collected both prey and fisher samples widely across northern Wisconsin, they should experience similar variability in isotopic values. We sampled nine potential food items: short-tailed shrews *B. brevicauda* ($n=11$), masked shrews *S. cinereus* ($n=5$), deer mice *Peromyscus maniculatus* ($n=10$), red squirrels *Tamiasciurus hudsonicus* ($n=12$), ruffed grouse *Bonasa umbellus* ($n=7$), white-tailed deer *Odocoileus virginianus* ($n=18$), woodpeckers ($n=4$), acorns *Quercus* sp. ($n=12$), and berries (*Rubus* sp., *Vaccinium* sp., *Prunus virginiana*, $n=60$). Additionally, we obtained porcupine *E. dorsatum* ($n=6$) hair samples from central Wisconsin, and used snowshoe hare *L. americanus* isotopic signatures from Roth et al. (2007). Specifically, we simulated snowshoe hare signatures in R package ver. 3.1.1, randomly selected 10 samples, and subsequently calculated a mean and standard deviation from this simulated dataset.

Stable isotope preparation and analysis

Stable isotope analysis has become a useful technique in wildlife foraging studies because not only can diet contributions be estimated from consumer tissues such as hair, it also avoids biases of digestibility associated with traditional diet reconstruction methods (Ben-David and Flaherty 2012). We prepared all fisher and diet samples using standard techniques described in Pauli et al. (2009). We provide results as ratios in parts per thousand relative to international standards, Vienna-Peedee Belemnite and atmospheric nitrogen. We corrected for trophic discrimination with values established by Roth and Hobson (2000) for red foxes *Vulpes vulpes*, 2.6‰ for ^{13}C and 3.4‰ for ^{15}N .

Isotopic analysis is only useful when diet groups are distinct (Ben-David and Flaherty 2012); thus, we first determined which prey could be distinguished isotopically from one another. We used a K nearest-neighbor randomization to define isotopically distinct prey groups (all pairwise $p < 0.05$; Rosing et al. 1998) as: 1) shrews, mice, squirrels, and porcupines; 2) deer, grouse, and snowshoe hares; 3) nuts and berries; and 4) other birds. To estimate the proportional importance of each prey group to fisher diet we used Bayesian mixing models in the package ‘stable isotope analysis’ in R ver. 4 (SIAR; Parnell et al. 2010). We ran uninformed models, parameterized with uniform priors (evenly distributed among prey groups), and incorporating trophic discrimination and concentration dependence. We expressed outputs as means of probability density functions, representing each prey group's probable contribution to diet (Parnell et al. 2010). We further compared raw isotope values between sexes using a Welch's t-test, and across ages with linear regression. We also report fisher diets from Ontario, Michigan and Minnesota. Ontario ($n=270$, Clem 1977; $n=57$, deVos 1952) and Michigan ($n=35$, Powell 1977) fisher diets were reported as percent occurrence of each prey type in GI tracts or scats. Minnesota fisher diets ($n=1649$, Kuehn 1989) were reported as the aggregate percentage of total prey weight in stomachs. We grouped prey type into similar categories as identified in this study, and due to differences in diet reconstruction methods among studies, we present a qualitative, rather than quantitative comparison.

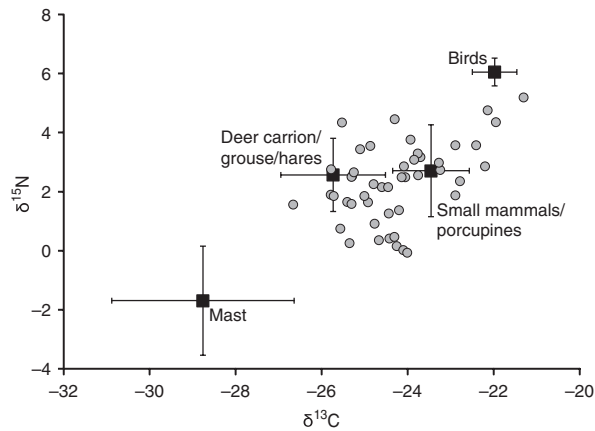


Figure 1. Isotopic signatures of fisher *Pekania pennanti* hair (circles) collected during 2013 and signatures for prey groups (mean ± 1 SD) from northern Wisconsin, USA. Fisher samples were corrected with trophic discrimination factors of 3.4‰ for $\delta^{15}\text{N}$ and 2.6‰ for $\delta^{13}\text{C}$.

Body condition analysis

To assess the body condition of fishers and to explore its relationship to diet, we compared the condition of a contemporary population to that of a historical population and two regional populations. We weighed thawed fresh mass of omentum fat samples for contemporary fishers from northern Wisconsin, and estimated percent body fat for each individual using a previously developed model (Robitaille and Jensen 2005). Although Robitaille and Jensen (2005) examined percent omentum fat for both males and females, only the male-specific model was significant. Additionally, because females are constrained by their smaller structural size, males are more likely to experience changes in body fat with different food availabilities (Powell 1979, Holmes and Powell 1994). Consequently, we only considered males in subsequent analyses. We then compared these mean estimates of percent fat to fishers collected from Wisconsin during the 1990s (Gilbert 2000) and to fishers collected from two regional populations in Canada (Garant and Crête 1999, Robitaille and Jensen 2005). All fishers were sampled mid-fall through the winter during trapping seasons. Though the

body condition methods differed among studies, Robitaille and Jensen (2005) demonstrated that different fat depots (e.g. omentum, kidney) are reliable estimates of percent body fat for individuals. Consequently, we used each study's estimated percent body fat for comparisons among populations. Gilbert (2000) derived percent body fat via kidney fat depots for 250 male fishers collected throughout their range in Wisconsin in 1992. To maintain similar sample sizes in our comparison, we randomly subsampled 30 individuals from this historical Wisconsin population. Garant and Crête (1999) and Robitaille and Jensen (2005) calculated percent body fat from whole carcasses (Québec 1991–1992, $n=34$, Garant and Crête 1999; Ontario 1998–2000, $n=86$, Robitaille and Jensen 2005). Finally, to examine whether diet is related to nutritional condition, we compared nitrogen isotopic signature and percent body fat within the contemporary fisher population using linear regression.

Results

Fisher hair exhibited great variation in isotopic signatures (Fig. 1), though males and females did not differ in either $\delta^{13}\text{C}$ ($t_{42,2}=0.63$, $p=0.53$) or $\delta^{15}\text{N}$ ($t_{31,4}=1.14$, $p=0.26$). We found no effect of age on $\delta^{15}\text{N}$ ($F_{1,43}=0.63$, $p=0.43$), but a slight positive relationship between age and $\delta^{13}\text{C}$ ($\beta=0.26$, $F_{1,43}=5.47$, $p=0.02$). We found no differences in overall diet between sexes or age classes, so we present the population-wide diet. Mixing models revealed that the shrew, mouse, squirrel, and porcupine group represented the highest mean proportion of fisher diet, accounting for 63% of assimilated diet. Deer carrion, grouse, and hares made up the second highest proportion of diet (25%) (Table 1). Past studies from Michigan, Minnesota and Ontario indicated higher reliances of fishers on deer, hares and grouse compared to our estimates from Wisconsin.

Contemporary Wisconsin male fishers ($n=28$) averaged 6.6% body fat (± 0.78 , 95% CI), which was less than the average for male fishers observed 20 years ago in Wisconsin ($\bar{x}=11.7\% \pm 2.40$); and for fishers in Québec ($\bar{x}=11.4\% \pm 0.40$) and Ontario ($\bar{x}=8.4\% \pm 0.63$; Fig. 2). The 95% confidence intervals for the contemporary population did not overlap with confidence intervals for the other populations.

Table 1. Mean proportion of assimilated diet groups (95% credible intervals) in fishers *Pekania pennanti* in Wisconsin, fall 2013, estimated via uninformed Bayesian mixing models. Also shown are summarized fisher diet studies from Ontario (ON), Michigan (MI) and Minnesota (MN), reported by Powell 1993. Estimates are grouped into same diet categories as the contemporary study and shown as proportion of GI tracts or scat containing each prey type for the Michigan and Ontario studies, and proportion of total weight of prey from stomach contents for the Minnesota study.

Diet groups	WI ^a	ON ^b	ON ^c	MI ^d	MN ^e
Small mammals/porcupines	0.63 (0.45–0.80)	0.51	0.55	0.62	0.00
Deer carrion/grouse/hares	0.25 (0.01–0.48)	0.34	0.70	0.51	0.45
Mast	0.08 (0.0–0.18)	0.00	0.00	0.06	0.00
Birds	0.03 (0.0–0.08)	0.12	0.07	0.00	0.00
Other mammals (e.g. muskrat)		0.18	0.13	0.14	0.12
Unidentified vertebrates		0.13	0.12	0.00	0.34
Arthropods		0.00	0.21	0.00	0.00

^athis study, mean proportion of assimilated prey groups from isotopic mixing models

^bClem 1977, proportion of GI tracts containing prey, averaged between males and females

^cdeVos 1952, proportion of GI tracts containing prey

^dPowell 1977, proportion of scats containing prey

^eKuehn 1989, proportion of total weight of prey from stomachs, averaged between males and females

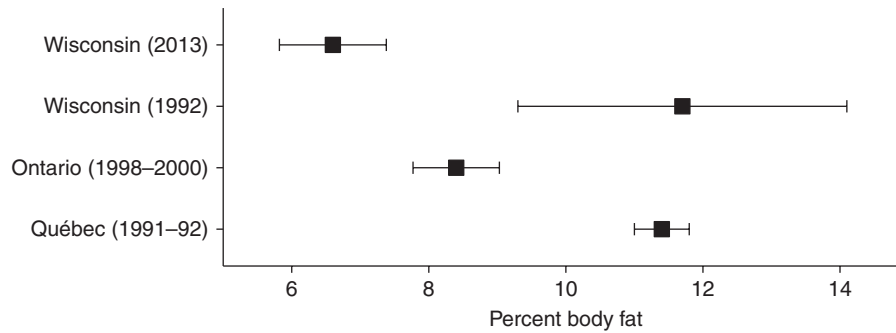


Figure 2. Mean percent body fat (\pm 95% CI) of four male fisher *Pekania pennanti* populations (Wisconsin 2013, $n=28$; Wisconsin 1992, $n=30$; Ontario 1998–2000, $n=86$; Québec 1991–1992, $n=34$).

Additionally, we did not detect a relationship between percent body fat and $\delta^{15}\text{N}$ in contemporary Wisconsin fishers ($F_{1,24} = 0.05$, $p = 0.82$).

Discussion

Our isotopic analyses revealed that diet across individual fishers in northern Wisconsin was variable during autumn and early winter 2013, as would be expected of a generalist consumer. For the fisher population, small mammals (shrews, mice, squirrels) and porcupines made up the most used diet group, constituting the highest proportion of assimilated diet. The proportion of diet estimated for larger-bodied prey (deer, grouse, hares) has a substantially lower mean, but the credible interval overlaps with that of smaller-bodied prey, indicating uncertainty in the diet reconstruction. Thus, fishers from Wisconsin in 2013 appear to be consuming similar diets to those found in other systems, where the breadth of prey eaten by fishers was great and commonly consisted of medium to small rodents, porcupines, and hares (Powell 1993). Fishers do not appear to be relying heavily on carrion, despite a large deer population ($>25\,000$ deer harvested each year in northern Wisconsin). This is somewhat surprising considering recent work suggested martens, the smaller relative of fishers, were consuming large quantities of deer carrion in the same area (Carlson et al. 2014).

The average percent body fat of male fishers in 2013 was lower than those from two decades ago as well as compared to fishers sampled in Canada. The lowered fat reserves would be consistent with using more small-bodied prey. Unfortunately, we are unable to separate isotopically either hares from deer or porcupines from the small mammals group to determine how much of the assimilated diet is composed of each of these prey items individually. Because the isotopic signatures of the prey species overlap in this study, traditional diet reconstruction techniques could aid in further distinguishing the contribution of important prey species like porcupines to fishers' diet.

Historical harvest records suggest that fishers were less common in northern Wisconsin than in the hardwood timber stands of central and southern Wisconsin (Schorger 1942). Thus, prior to their extirpation, fishers appear not to have been particularly abundant in the northernmost regions of Wisconsin. After reintroduction, the apparent rapid growth in the fisher population could have resulted from abundant naive prey in regenerating forests coupled

with low density of competitors (Fryxell et al. 1999). The recent harvest and winter track survey data suggest that the fisher population in northern Wisconsin may again be decreasing (Rolley et al. 2013). Our study demonstrates that this population is also in lower body condition than previously reported, and that despite a highly variable diet like other populations, these fishers may be consuming fewer large-bodied prey than expected. Although our single year dataset cannot disentangle the mechanisms of the purported decline in this population, our estimates of low body fat and a diet consisting largely of small-bodied prey suggests that nutritional energetics could be a contributing factor, and warrants future monitoring.

Acknowledgements – We are especially grateful to G. Albers, J. Carlson, J. Merten and P. Manlick for assistance in gathering samples and sharing data.

Funding – Funding for this study was provided by Wisconsin Dept of Natural Resources, Great Lakes Indian Fish and Wildlife Commission, and Wisconsin Trappers Association.

References

- Ben-David, M. and Flaherty, E. A. 2012. Stable isotopes in mammalian research: a beginner's guide. – *J. Mammal.* 93: 312–328.
- Berg, W. E. and Kuehn, D. W. 1994. Fishers and American martens in a changing landscape. – In: Buskirk, S. W. et al. (eds), *Martens, sables, and fishers: biology and conservation*. Cornell Univ. Press, pp. 262–271.
- Bowman, J. et al. 2006. Numerical response of fishers to synchronous prey dynamics. – *J. Mammal.* 87: 480–484.
- Boyles, J. B. and Storm, J. J. 2007. The perils of picky eating: extinction risk correlates with dietary breadth in insectivorous bats. – *PLoS One* 7: e672.
- Bulmer, M. G. 1974. A statistical analysis of the 10-year cycle in Canada. – *J. Anim. Ecol.* 43: 609–622.
- Buskirk, S. W. and Harlow, H. J. 1989. Body-fat dynamics of the American marten (*Martes americana*) in winter. – *J. Mammal.* 70: 191–193.
- Buskirk, S. W. and Ruggiero, L. F. 1994. American marten. – In: Ruggiero, L. F. et al. (eds), *The scientific basis for conserving forest carnivores: American marten, fisher, lynx and wolverine*. US Dept of Agriculture Forest Service, Gen. Tech. Rep. RM-254, pp. 7–37.
- Carlson, J. E. et al. 2014. Potential role of prey in the recovery of American martens to Wisconsin. – *J. Wildl. Manage.* 78: 1499–1504.

- Chapron, G. et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. – *Science* 346: 1517–1519.
- Clem, M. K. 1977. Interspecific relationship of fisher and martens in Ontario during winter. – In: Phillips, R. L. and Jonkel, C. J. (eds), *Proc. 1975 Predator Symp.*, Montana For. Conserv. Exp. Stn, pp. 165–182.
- DeCalesta, D. S. et al. 1975. Starving and refeeding mule deer. – *J. Wildl. Manage.* 39: 663–669.
- deVos, A. 1952. Ecology and management of fisher and marten in Ontario. – Ontario Dept of Lands and Forests Tech. Bull., Peterborough, ON, Canada.
- Erwin, D. H. 1998. The end and beginning: recoveries from mass extinctions. – *Trends Ecol. Evol.* 13: 344–349.
- Fryxell, J. M. et al. 1999. Density dependence, prey dependence, and population dynamics of martens in Ontario. – *Ecology* 80: 1311–1321.
- Garant, Y. and Crête, M. 1999. Prediction of water, fat and protein content of fisher carcasses. – *Wildl. Soc. Bull.* 27: 403–408.
- Gilbert, J. H. 2000. Impact of reestablished fisher populations on Wisconsin's bobcat population. – PhD thesis, Univ. of Wisconsin, Madison, WI.
- Helldin, J. O. 1999. Diet, body condition, and reproduction of Eurasian pine martens (*Martes martes*) during cycles in microtine density. – *Ecography* 22: 324–336.
- Holmes, T. and Powell, R. A. 1994. Morphology, ecology and the evolution of sexual dimorphism in North American Martes. – In: Buskirk, S. W. et al. (eds), *Martens, sables and fishers: biology and conservation*. Cornell Univ. Press, pp. 72–84.
- Jensen, P. G. et al. 2012. Marten and fisher responses to fluctuations in prey populations and mast crops in the northern hardwood forest. – *J. Wildl. Manage.* 76: 489–502.
- Kuehn, D. W. 1989. Winter foods of fishers during a snowshoe hare decline. – *J. Wildl. Manage.* 53: 688–692.
- LaPoint, S. D. et al. 2015. Mesopredator release facilitates range expansion in fisher. – *Anim. Conserv.* 18: 50–61.
- Lewis, J. C. et al. 2012. Carnivore translocations and conservation: insights from population models and field data for fishers (*Martes pennanti*). – *PLoS One* 7: e32726.
- Leonard, R. D. 1980. Winter activity and movements, winter diet and breeding biology of the fisher in southeast Manitoba. – MS thesis, Univ. of Manitoba, Winnipeg, MB, Canada.
- Linnell, J. D. C. et al. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. – *Anim. Conserv.* 4: 345–349.
- Martin, S. K. 1994. Feeding ecology of American martens and fishers. – In: Buskirk, S. W. et al. (eds), *Martens, sables, and fishers: biology and conservation*. Cornell Univ. Press, pp. 297–315.
- McKinney, M. L. and Lockwood, J. L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. – *Trends Ecol. Evol.* 14: 450–453.
- Myers, P. et al. 2009. Climate-induced changes in the small mammal communities of the northern Great Lakes region. – *Global Change Biol.* 15: 1434–1454.
- Mustonen, A.-M. et al. 2015. Development of indices to estimate fat reserves in the wild American mink (*Neovison vison*). – *Mammal. Res.* 60: 245–254.
- Parnell, A. C. et al. 2010. Source partitioning using stable isotopes: coping with too much variation. – *PLoS One* 5: e9672.
- Pauli, J. N. et al. 2009. An isotopic technique to mark mid-sized vertebrates non-invasively. – *J. Zool.* 278: 141–148.
- Pokallus, J. W. and Pauli, J. N. 2015. Population dynamics of a northern-adapted mammal: disentangling the influence of predation and climate change. – *Ecol. Appl.* 25: 1546–1556.
- Powell, R. A. 1977. Hunting behavior, ecological energetics and predator – prey community: stability of the fisher (*Martes pennanti*). – PhD thesis, Univ. of Chicago, IL.
- Powell, R. A. 1979. Ecological energetics and foraging strategies of the fisher (*Martes pennanti*). – *J. Anim. Ecol.* 48: 195–212.
- Powell, R. A. 1993. The fisher: life history, ecology and behavior. – Univ. of Minnesota Press.
- Powell, R. A. et al. 2017. The fisher as a model organism. – In: Macdonald, D. W. et al. (eds), *Biology and conservation of mustelids*. Oxford Univ. Press.
- Powell, R. A. and Zielinski, W. J. 1994. Fisher. – In: Ruggiero, L. F. et al. (eds), *The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine*. US Dept of Agriculture Forest Service, Gen. Tech. Rep. RM-254, pp. 38–73.
- Ripple, W. J. et al. 2014. Status and ecological effects of the world's largest carnivores. – *Science* 343: 151–163.
- Robitaille, J.-F. and Cobb, E. W. 2003. Indices to estimate fat depots in American marten (*Martes americana*). – *Wildl. Biol.* 9: 113–121.
- Robitaille, J.-F. and Jensen, K. 2005. Additional indices to estimate fat contents in fisher (*Martes pennanti*) populations. – *Wildl. Biol.* 11: 263–269.
- Rolley, R. E. et al. 2013. Fisher population analysis. – Wisconsin Dept of Natural Resources.
- Rosing, M. N. et al. 1998. Analysis of stable isotope data: a K nearest-neighbors randomization test. – *J. Wildl. Manage.* 62: 380–388.
- Roth, J. D. and Hobson, K. A. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. – *Can. J. Zool.* 78: 848–852.
- Roth, J. D. et al. 2007. Geographical gradients in diet affect population dynamics of Canada lynx. – *Ecology* 88: 2736–2743.
- Schorger, A. W. 1942. Extinct and endangered mammals and birds of the Great Lakes region. – *Trans. Wisconsin Acad. Sci. Arts Letters* 34: 26–28.
- Schulte-Hostedde, A. I. et al. 2005. Restitution of mass/size residuals: validating body condition indices. – *Ecology* 86: 155–163.
- Sultaire, S. M. et al. 2016. Climate change surpasses land use change in the contracting range boundary of a winter-adapted mammal. – *Proc. R. Soc. B.* 283: 20153104.
- Williams, B. W. et al. 2007. Historical perspective on the reintroduction of the fisher and American marten in Wisconsin and Michigan. – US Dept of Agriculture Forest Service Northern Research Station Gen. Tech. Rep. NRS-5.
- Zielinski, W. J. and Duncan, N. P. 2004. Diets of sympatric populations of American martens (*Martes americana*) and fishers (*Martes pennanti*) in California. – *J. Mammal.* 85: 470–477.