



## Note

# Fisher Predation on Canada Lynx in the Northeastern United States

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**ABSTRACT** The geographic range of Canada lynx (*Lynx canadensis*) extends south from Canada into the United States where they are federally protected as a threatened species. Although inadequate protection of habitat on federal lands was the primary reason for listing, the status of lynx in the lower 48 states is not well understood. Thus, we initiated a telemetry study to assess the status of a lynx population in northern Maine, USA. In this manuscript, we present findings on a source of mortality not previously documented. Between 1999 and 2011, we captured 187 lynx, equipped 85 with radio-collars, and investigated mortalities when they occurred. Predation was the leading source of mortality and accounted for  $\geq 18$  of 65 mortalities, 14 of which were attributed to fishers (*Martes pennanti*). Although fisher predation did not appear to restrict population growth during this study, we recommend that lynx and fishers be monitored where the species coexist to better inform management decisions. © 2018 The Wildlife Society.

**KEY WORDS** Canada lynx, fisher, *Lynx canadensis*, Maine, *Martes pennanti*, mortality, necropsy, predation.

Canada lynx (*Lynx canadensis*) are distributed throughout the boreal forest of Canada and Alaska and their range extends into 14 northern-tier states. In 2000, lynx were protected as a threatened species in these states under the United States Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 2000) and in 2014 protection was extended to wherever they occurred in the contiguous United States (USFWS 2014). In their core range, lynx populations fluctuate in delayed synchrony with the abundance of their primary prey, snowshoe hare (*Lepus americanus*; Elton and Nicholson 1942, Keith 1963, O'Donoghue et al. 1997). At the time of federal listing, little was known about factors that may limit lynx numbers at the southern edge of their range.

In the core and peripheral range, starvation and predation are the leading sources of natural mortality for lynx (Koehler 1990, Poole 1994, Slough and Mowat 1996, O'Donoghue et al. 1997, Squires and Laurion 2000). Mountain lions (*Puma concolor*), wolverines (*Gulo gulo*), gray wolves (*Canis lupus*), and coyotes (*C. latrans*) are documented predators of

lynx (O'Donoghue et al. 1995, 1997; Slough and Mowat 1996; Squires and Laurion 2000). Intraspecific predation among lynx has also been documented (Else 1954). At the southern edge of lynx range where there is a more diverse carnivore guild, increased competition may lead to higher mortality and could limit lynx numbers (Parker et al. 1983, Buskirk et al. 2000). In Maine, potential predators of lynx include coyotes and other lynx, which have been confirmed elsewhere, and black bears (*Ursus americanus*), bobcats (*L. rufus*), and fishers (*Martes pennanti*), which have not been previously documented as predators of lynx.

In 1999, we initiated a telemetry study in northern Maine where the objective was to broaden our understanding of a southern lynx population and to determine if mortality was a limiting factor in Maine. Our hypothesis was that mortality sources would be similar to those documented in the Canadian boreal forests, and that mortality rates would fluctuate with the snowshoe hare population.

## STUDY AREA

The study area encompassed 4 townships (386 km<sup>2</sup>) in the Musquacook Lakes region of northwestern Maine (Fig. 1). The area ranges in elevation from 250 m to 550 m and is characterized by rolling hills and wide valleys. Regenerating red spruce (*Picea rubens*), white spruce (*P. glauca*), and balsam fir (*Abies balsamea*) stands dominated the area. This spruce-fir forest was interspersed with lowlands comprised of black spruce (*P. mariana*), tamarack (*Larix laricina*), and northern white cedar (*Thuja occidentalis*) and ridges dominated by

Received: 5 September 2017; Accepted: 5 June 2018

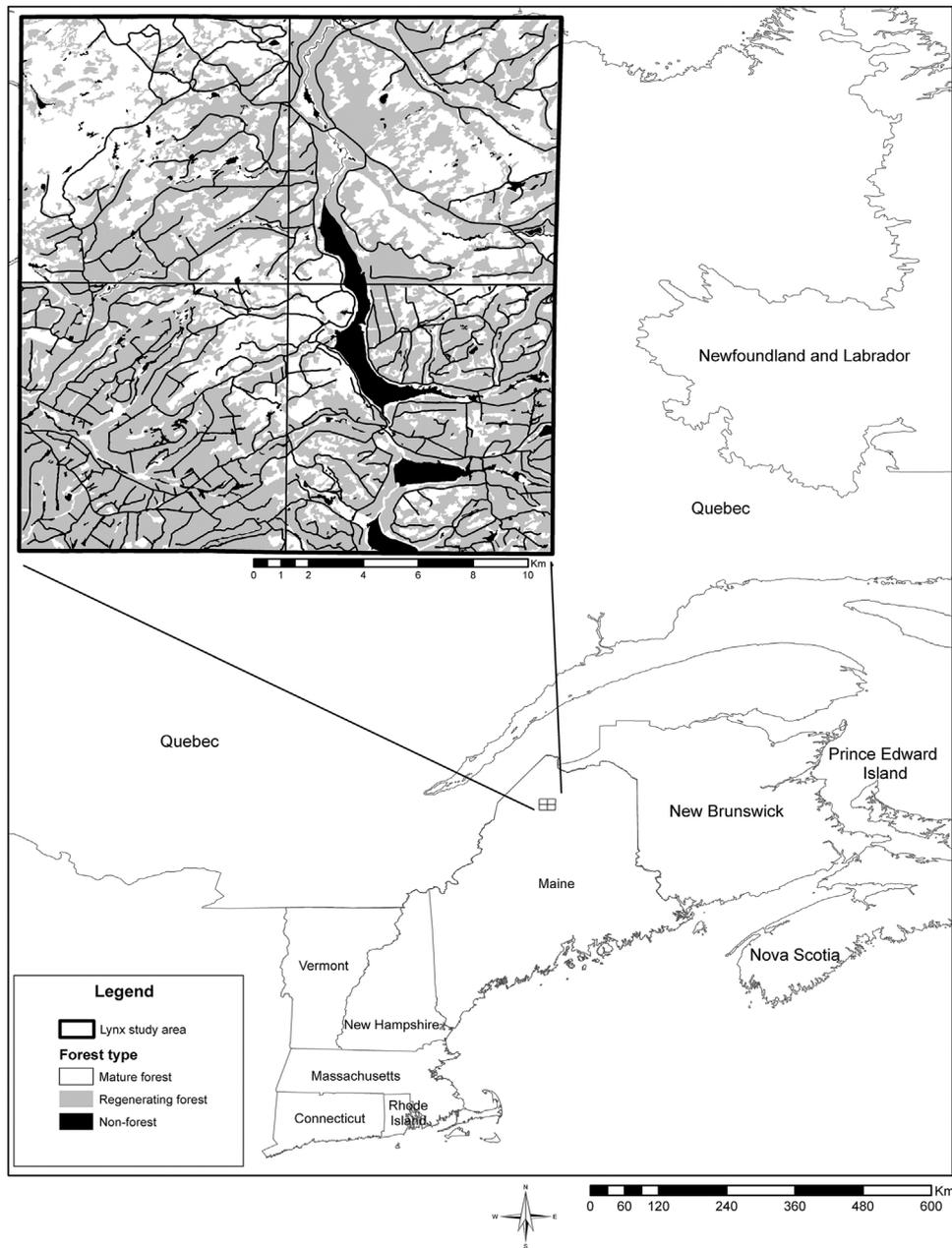
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**Figure 1.** The 400-km<sup>2</sup> study area where we researched Canada lynx on a commercial forest in northern Maine, USA, 1999 and 2011.

sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), yellow birch (*B. alleghaniensis*), and gray birch (*B. populifolia*). Much of the study area (~46% or 17,562 ha) was clear-cut in the 1980s to salvage trees harmed by the spruce-budworm (*Choristoneura fumiferana*) epizootic and to prevent further expansion of the outbreak. As a result, most of these stands were regenerating spruce and fir. Mature stands of conifer forest comprised only 12% of the study area and were typically associated with riparian zones. Dominant fauna in the study area that may have directly or indirectly affected lynx included moose (*Alces alces*), deer (*Odocoileus virginianus*), black bear, coyote, red fox (*Vulpes vulpes*), fisher, American marten (*Martes americana*), snowshoe hare, North American red squirrel (*Tamiasciurus hudsonicus*), and ruffed

grouse (*Bonasa umbellus*). Nearly half of Maine's 6.8 million ha of forest, most of Maine's lynx range, and our entire study area was owned by large timber companies that intensively managed their land for forest products (Seymour and Hunter 1992). Land-management activities in the study area included timber harvesting, herbicide applications to promote conifer regeneration, precommercial thinning to enhance stand growth, and road construction. The land was privately owned, but public access was allowed and regulated by the North Maine Woods Association, a non-profit organization of landowners established to manage access on 1.4 million ha of private forestland in northern Maine. Human settlements were limited to seasonal camps and logging operations, and most roads were unimproved dirt

roads used primarily for tree harvest and extraction. During winter, this area was largely inaccessible to the public because roads were only plowed to harvest trees and extract wood. In addition, the study area did not have maintained snowmobile trails. Although snowfall can occur between October and May, snow accumulation was most common from December through April. Between 1999 and 2011, average monthly snow depth at winter severity stations monitored near our study area was 64.8 cm with the highest monthly snow depths in February and March (81.3 cm and 91.4 cm, respectively) and the lowest monthly snow depth in December (34.3 cm; Maine Department of Inland Fisheries and Wildlife [MDIFW], unpublished data).

## METHODS

Between 1999 and 2011, we captured and equipped lynx with very high frequency (VHF) collars as described in Vashon et al. (2008a) or global positioning system (GPS) collars (Lotek Wireless, New Market, Ontario, Canada). Animal capture and handling procedures conformed to guidelines established by the American Society of Mammalogists (American Society of Mammalogists 1998). All collars were equipped with a 4-hour mortality sensor; as weather permitted we monitored collars twice per week from fixed-wing aircraft. When we detected a mortality signal, we located the dead lynx, photographed the site, and collected data and lynx remains, if available. We estimated the time of death as the midpoint between the last active VHF signal and the first inactive signal (i.e., mortality signal), unless other factors (e.g., weather event, lack of rigor mortis, activity sensor on GPS collars) could pinpoint a more accurate time of death.

We sent lynx carcasses without signs of trauma to a pathologist for a complete necropsy to determine cause of death (e.g., starvation cases were determined based on body and bone marrow condition). We performed necropsies of lynx carcasses with visible signs of trauma to determine the cause and extent of the injury. We examined femur bone marrow when it was available and assigned a health rating

(i.e., healthy, fair, poor) as described in Cheatum (1949). We identified predation as the cause of death if we found pre-mortem hemorrhaging associated with canine tooth punctures on lynx carcasses. We assigned wider canine punctures that were part of a 4-puncture pattern as upper canines and narrower canine punctures as the lower canines. However, as noted by Wade and Bowns (1985), obtaining accurate intercanine width measurements was sometimes difficult because of tissue pliancy, extensive tissue trauma, and repeated biting. In addition, canines were commonly missing or broken on live-captured fishers that we handled during this study, and on fisher skulls that we examined from fur trappers (MDIFW, unpublished data). Thus, locating 4 perfectly matched canine punctures to measure and assign as upper and lower canines was sometimes challenging. When this occurred, we measured the canine punctures but did not assign them as upper or lower (Table 1). We determined the species of predator by comparing these data with the intercanine width measurements from previously measured predator skulls (Elbroch 2006; Table 2). Because bobcats were rare in the study area (i.e., 1 bobcat captured during the 12-yr study) and black bears were hibernating when mortalities occurred, we did not include bobcat or black bear intercanine width measurements in our comparisons. We identified the predator when intercanine width measurements were consistent with one species and did not overlap with other predator species.

We also identified predation as the cause of death if we found predator tracks in the snow leading to a resting lynx or observed the tracks of a lynx being chased by a predator that ended at the kill site. A kill site was a disturbed area in the snow where tracks and scratch marks showed that a struggle between 2 animals had occurred, often with broken branches, blood, and tufts of lynx hair. In these cases, we identified the species of predator based on track characteristics, measurements, and trail pattern.

We classified the species of predator as unknown if we were unable to obtain accurate measurements of the canine punctures and if tracks and other sign at the mortality site

**Table 1.** Nineteen of 20 intercanine width measurements from 6 Canada lynx carcasses in northern Maine, USA, 1999 and 2011 that fell within the range reported for fishers and did not overlap intercanine width measurements of coyote or lynx (Elbroch 2006).

| Lynx identification | Lower canine measurements (mm) | Upper canine measurements (mm) | Not assigned <sup>a</sup> (mm) |
|---------------------|--------------------------------|--------------------------------|--------------------------------|
| L93a                | 12                             |                                |                                |
| L93b                | 8                              |                                |                                |
| L38a                | 11.2                           | 18                             |                                |
| L38b                | 11.8                           | 20                             |                                |
| L125                | 13                             |                                |                                |
| L38c                | 11.8                           | 13.5                           |                                |
| L8a                 |                                |                                | 14.1                           |
| L8b                 |                                |                                | 21.6                           |
| L8c                 |                                |                                | 15.8                           |
| L36                 |                                |                                | 16.8                           |
| L38d                | 18                             | 21.3                           |                                |
| L38e                | 17.3                           | 21.7                           |                                |
| L38f                | 17.7                           | 23.9                           |                                |
| L157                |                                |                                | 16                             |

<sup>a</sup> Unable to assign canine punctures as upper or lower because of trauma and repeated biting or because we were not able to locate 4 matching canine punctures (e.g., 3 canine punctures, suggesting predator had a broken or missing canine).

**Table 2.** Median intercanine width measurements of male and female carnivores in North America (Elbroch 2006) that were possible predators of lynx in northern Maine, USA, 1999 and 2011.

| Age class, sex, and species | Lower intercanine measurement (mm) |           |          | Upper intercanine measurement (mm) |           |          |
|-----------------------------|------------------------------------|-----------|----------|------------------------------------|-----------|----------|
|                             | Median                             | Range     | <i>n</i> | Median                             | Range     | <i>n</i> |
| Adult female fisher         | 13.2                               | 11.9–16.2 | 13       | 15.0                               | 13.1–17.1 | 14       |
| Adult male fisher           | 15.8                               | 13.6–17.6 | 17       | 18.0                               | 15.0–22.0 | 18       |
| Adult female lynx           | 23.4                               | 22.3–24.4 | 10       | 24.5                               | 22.7–25.7 | 10       |
| Adult male lynx             | 23.6                               | 21.9–27.8 | 10       | 25.4                               | 23.7–27.6 | 10       |
| Adult female coyote         | 28.2                               | 25.5–29.5 | 5        | 30.4                               | 27.1–32.2 | 4        |
| Adult male coyote           | 30.3                               | 27.0–35.1 | 6        | 33.2                               | 31.0–35.9 | 6        |

were obscured by changing weather conditions. However, if some sign was evident, we classified the predator that killed the lynx as the species whose sign was present at the site.

We identified the habitat characteristics associated with predation losses from stand-level data provided by the landowners and developed a geographic information system (GIS) base layer from their vector coverages (Vashon et al. 2008b). We classified forested stands by cover type (conifer, deciduous, mixed conifer, and mixed deciduous), dominant species, stand age (mature  $\geq 40$  yr and regenerating  $< 40$  yr), stand height class (0–4.3 m, 4.4–7.6 m, 7.7–12.2 m, and 12.3–18.3 m), and canopy closure (0–24%, 25–50%, 51–80%, and 81–100%). We verified stand map classification with habitat notes recorded at the mortality site.

## RESULTS

We captured 187 lynx (83 females, 104 males) and equipped 85 with radio-collars (41 females, 44 males) between 1999 and 2011. The mean weight of adult male and female lynx was 11.3 kg (range = 8.2–15.0 kg,  $n = 101$ ) and 9.0 kg (range = 7.0–10.5 kg,  $n = 58$ ), respectively. We documented the mortality of 65 lynx including 61 collared lynx, 1 unmarked kitten of a collared female, and 3 ear-tagged lynx. We determined that 18 lynx were killed by predators, 17 died of starvation, 17 from undetermined causes, 12 from human factors (e.g., vehicle collisions), and 1 from hyperthyroidism (Table 3). We determined that fishers had killed 14 lynx (9 females, 5 males) and likely killed 2 additional lynx (2 females). We could not determine the species of predator for the remaining 2 lynx (1 female, 1 male; Table 4).

Thirteen of the 14 lynx killed by fishers were adults with established home ranges, and weights and bone marrow indicated that these lynx were healthy or in fair condition

(Table 5). The mean weight (8.2 kg) of 3 adult lynx that were recovered before the predator could consume the carcass was similar to the mean weight of adult lynx captured in this study. We also recorded partial carcass weights ( $\bar{x} = 5.4$  kg) from 6 adult lynx killed by fishers that were comparable to the mean weight of whole carcasses of lynx that died of starvation ( $\bar{x} = 5.9$  kg,  $n = 16$ ).

The majority of mortalities occurred during winter when tracks and other sign allowed us to recreate the event. At 12 mortality sites, we observed where 10 lynx had been resting in a bed when killed by a fisher ( $n = 10$ ) or where lynx had been chased by a fisher and killed ( $n = 2$ ). The only predator tracks at these sites were from fishers, and on 7 occasions, we observed where the fisher had dragged and then cached the lynx (Table 4). Drag marks ranged from 1 m to 201 m. We often observed bright, red drops of blood peppered along this drag mark. Caching sites included tree cavities, root masses, hollow logs, the space underneath downed trees or dense conifer vegetation, and sometimes buried under the snowpack with no associated structure nearby. There were usually numerous fisher scats and a network of fisher trails to and from the carcass. We also observed a fisher in a cavity with the remains of a lynx carcass (L44), and on 2 occasions, we found dark brown guard hairs inside the mouth of the dead lynx (L114 and L174). Perhaps most noteworthy was the absence of other predator tracks and sign.

During necropsy, we found pre-mortem hemorrhaging and canine punctures on the head, neck or throat of 9 of 18 lynx. On 6 lynx (5 females, 1 male), 19 of 20 upper and lower intercanine width measurements fell within the range reported for fishers and did not fall within the upper or lower bounds reported for coyotes or lynx (Table 2), thus confirming our field observations that a fisher had attacked and killed these lynx.

Although only 12% of the study area was classified as mature conifer, the majority of lynx killed by fishers (86%) died in mature conifer stands. Most of these stands (75%) were dominated by northern white cedar or black spruce with canopy heights of 12.3–18.3 m and canopy closures between 25% and 50%. One lynx was killed in a regenerating stand of conifer that was dominated by balsam fir and red spruce and 1 lynx was killed in a mature deciduous stand dominated by red maple and yellow birch (Table 6). The remaining 4 lynx, where we could not ascertain the species of predator, were killed in mature conifer stands dominated by northern white cedar.

**Table 3.** Mortality sources of 65 Canada lynx in northern Maine, USA, 1999 and 2011.

| Mortality source              | <i>n</i> |
|-------------------------------|----------|
| Predation by fisher           | 14       |
| Predation by unknown predator | 2        |
| Likely predation by fisher    | 2        |
| Starvation                    | 17       |
| Undetermined                  | 17       |
| Legal harvest in Canada       | 7        |
| Illegal harvest               | 3        |
| Vehicle collision             | 2        |
| Disease (hyperthyroidism)     | 1        |

**Table 4.** Necropsy findings and field evidence of 18 Canada lynx that were killed by predators in northern Maine, USA, 1999 and 2011.

| Lynx identification | Number of days <sup>a</sup> | Carcass | Premortem hemorrhaging on neck and head | Premortem hemorrhaging with canine punctures | Canine punctures consistent with fisher | Ambushed and killed in bed <sup>b</sup> | Chase ending with kill <sup>c</sup> | Only fisher tracks at kill site | Drag marks to cached lynx | Dark brown hair in lynx mouth | Predator         |
|---------------------|-----------------------------|---------|---|--|---|---|-------------------------------------|---------------------------------|---------------------------|-------------------------------|------------------|
| L6                  | 2                           | Partial |   |  |   | •                                       |                                     | •                               | •                         |                               | Fisher           |
| L8 <sup>d</sup>     | 2                           | Whole   | •                                       | •  | •                                       | •                                       |                                     | •                               |                           |                               | Fisher           |
| L36                 | 2                           | Whole   | •                                       | •  | •                                       | •                                       |                                     | •                               | •                         |                               | Fisher           |
| L125                | 4                           | Partial | •                                       | •  | •                                       | •                                       |                                     | •                               |                           |                               | Fisher           |
| L157                | 1                           | Partial | •                                       | •  | •                                       |   | •                                   |                                 |                           |                               | Fisher           |
| L38                 | 13                          | Partial | •                                       | •  | •                                       |   |                                     | N/A <sup>e</sup>                |                           |                               | Fisher           |
| L93                 | 8                           | Partial | •                                       | •  | •                                       |   |                                     | •                               |                           |                               | Fisher           |
| L44                 | 3                           | Partial |   |  |   | •                                       |                                     | •                               | •                         |                               | Fisher           |
| L67                 | 1                           | Partial |   |  |   | •                                       |                                     | •                               | •                         |                               | Fisher           |
| L96                 | 7                           | Partial |   |  |   | •                                       |                                     | •                               | •                         |                               | Fisher           |
| L114                | 10                          | Partial | •                                       |  |   | •                                       |                                     | •                               | •                         | •                             | Fisher           |
| L137                | 3                           | Partial |   |  |   | •                                       |                                     | •                               | •                         |                               | Fisher           |
| L140                | 6                           | Partial |   |  |   | •                                       |                                     | •                               | •                         |                               | Fisher           |
| L156                | 4                           | Partial |   |  |   |   | •                                   | •                               |                           |                               | Fisher           |
| L168                | 2                           | Partial | •                                       |  |   |   |                                     | •                               | •                         |                               | Possibly fisher  |
| L174                | 8                           | Whole   | •                                       | • <sup>f</sup>                               |   |   |                                     | N/A <sup>e</sup>                |                           | •                             | Possibly fisher  |
| L9                  | 5                           | Partial | •                                       | • <sup>g</sup>                               |   |   |                                     | N/A <sup>e</sup>                |                           |                               | Unknown predator |
| L155                | 7                           | Whole   | •                                       | • <sup>f</sup>                               |   |   |                                     | N/A <sup>e</sup>                |                           |                               | Unknown predator |

<sup>a</sup> Number of days between estimated mortality event and field investigation.

<sup>b</sup> Tracks of a fisher leading to a lynx bed that terminated with a kill.

<sup>c</sup> Tracks of a fisher chasing a running lynx that terminated with a kill.

<sup>d</sup> The partial carcass of a radio-collared female was found cached at the same site as the entire carcass of her uncollared kitten (L8).

<sup>e</sup> No predator tracks observed at the kill site because of bare ground or recent snowfall that obscured all tracks.

<sup>f</sup> Could not obtain accurate intercanine width measurements because of the amount of trauma and repeated biting that occurred during the attack.

<sup>g</sup> Only premortem hemorrhaging with canine punctures located on the right hind leg.

## DISCUSSION

This is the first study to document predation of lynx by fishers. Subsequent to this study, researchers in Minnesota found possible evidence of fishers killing lynx on 2 separate occasions (R. A. Moen, University of Minnesota, personal communication).

Others have also reported anecdotal observations of fishers killing lynx (Powell 1982; R. D. Weir, Ecosystems Branch Ministry of the Environment, personal communication).

Lynx have not been extensively studied at the edge of their geographic range where they coexist with fishers, which may

**Table 5.** Demographic information and body condition of 14 resident Canada lynx killed by fishers in northern Maine, USA, 1999 and 2011.

| Lynx identification | Sex | Age class | Cementum age | Date of estimated mortality | Status of carcass                           | Weight of remains (kg) | Bone marrow condition <sup>a</sup> |
|---------------------|-----|-----------|--------------|-----------------------------|---|------------------------|------------------------------------|
| L6                  | F   | Adult     | N/A          | 24 Jan 2000                 | Partial (head absent)                       | 5.9                    | Healthy                            |
| L8 <sup>b</sup>     | F   | Kitten    | 0 yr 8 mo    | 24 Jan 2000                 | Whole                                       | 6.2                    | Healthy                            |
| L36                 | F   | Adult     | Not aged     | 10 Jan 2002                 | Whole                                       | 7.9                    | Not collected                      |
| L38                 | F   | Adult     | 4 yr 6 mo    | 20 Nov 2002                 | Partial (head and neck present)             |                        | N/A                                |
| L44                 | F   | Adult     | 4 yr 9 mo    | 20 Feb 2007                 | Partial (4 legs present)                    |                        | Healthy to fair                    |
| L67                 | F   | Adult     | N/A          | 28 Jan 2006                 | Partial (head and legs absent)              | 5.0                    | Not collected                      |
| L93                 | F   | Adult     | 5 yr 8 mo    | 25 Jan 2009                 | Partial (head, neck, and 4 limbs present)   |                        | Not collected                      |
| L96                 | M   | Adult     | N/A          | 3 Feb 2007                  | Partial (front half of body absent)         | 5.4                    | Healthy                            |
| L125                | F   | Adult     | 4 yr 9 mo    | 13 Feb 2007                 | Partial (viscera and hindquarter absent)    | 5.8                    | Healthy                            |
| L114                | M   | Adult     | 5 yr 10 mo   | 10 Mar 2010                 | Partial (neck, head, hind quarters present) |                        | Fair                               |
| L137                | F   | Adult     | N/A          | 3 Feb 2007                  | Partial (head absent)                       | 5.3                    | Healthy                            |
| L140                | M   | Adult     | N/A          | 5 Mar 2009                  | Partial (clumps of hide present)            |                        | N/A                                |
| L156                | M   | Adult     | N/A          | 7 Apr 2009                  | Partial (legs and viscera present)          | 5.2                    | Fair                               |
| L157                | M   | Adult     | Not aged     | 15 Feb 2009                 | Partial (head, neck, and one leg present)   |                        | Healthy                            |

<sup>a</sup> Bone marrow was classified as healthy when white, solid, and waxy, malnourished (fair) when red and solid, and poor when red and gelatinous (Cheatum 1949).

<sup>b</sup> A kitten without a radio-collar was found cached at the same site as the partial carcass of its radiocollared mother, L6.

**Table 6.** Habitat associated with 14 mortality sites where fishers killed lynx in northern Maine, USA, 1999 and 2011.

| Lynx identification    | Stand age    | Cover type | Dominant species                | Tree height (m) | Canopy closure (%) |
|------------------------|--------------|------------|---------------------------------|-----------------|--------------------|
| L6 and L8 <sup>a</sup> | Mature       | Conifer    | Cedar, black spruce             | 12.3–18.3       | 51–80              |
| L36                    | Mature       | Deciduous  | Red maple, yellow birch         | 12.3–18.3       | 25–50              |
| L38                    | Mature       | Conifer    | Cedar                           | 7.7–12.2        | 81–100             |
| L44                    | Mature       | Conifer    | Balsam fir, black spruce        | 12.3–18.3       | 25–50              |
| L67                    | Mature       | Conifer    | Black spruce                    | 12.3–18.3       | 25–50              |
| L93                    | Mature       | Conifer    | Black spruce, cedar, balsam fir | 12.3–18.3       | 25–50              |
| L96                    | Mature       | Conifer    | Cedar, black spruce             | 12.3–18.3       | 25–50              |
| L114                   | Mature       | Conifer    | Cedar, black spruce             | 12.3–18.3       | 25–50              |
| L125                   | Mature       | Conifer    | Cedar, black spruce             | 12.3–18.3       | 25–50              |
| L137                   | Regenerating | Conifer    | Balsam fir, red spruce          | 7.7–12.2        | 51–80              |
| L140                   | Mature       | Conifer    | Cedar                           | 12.3–18.3       | 25–50              |
| L156                   | Mature       | Conifer    | Cedar                           | 12.3–18.3       | 25–50              |
| L157                   | Mature       | Conifer    | Cedar, black spruce             | 12.3–18.3       | 25–50              |

<sup>a</sup> Habitat description not available from stand maps but recorded at the mortality site.

explain why predation by fishers has not been previously documented. In addition, extensive changes to Maine's forest landscape during the last several decades likely influenced fisher abundance, spatial use, and interactions with lynx. Our study area was part of a 3.4 million ha forest that was clear-cut in the 1980s to salvage red spruce and balsam fir affected by the spruce budworm epizootic. By the late 1990s, regenerating spruce and fir forest was a dominant component of the landscape, providing ideal habitat conditions for snowshoe hares. The abundance of snowshoe hares in northern Maine's regenerating conifer clear-cuts (Homyack et al. 2007, Scott 2009, Olsen 2015) benefited lynx (Fuller et al. 2007, Vashon et al. 2008b) and possibly benefitted fishers, which may have contributed to overlapping populations of both species in this region. Although fishers have been described as generalist predators (Powell 1981, Zielinski et al. 1999, Bowman et al. 2006), they have also been specifically associated with snowshoe hares (Bulmer 1975, Powell 1981, Kuehn 1989) and have increased in response to snowshoe hare abundance (Bowman et al. 2006). Thus, snow depth identified as a limiting factor for fishers by Krohn et al. (1995) may have been mitigated by the abundance of snowshoe hares.

Temporal and spatial factors likely influenced predation rates because most confirmed predation losses occurred in mature conifer forest (86%) and often during a snow event. Conversely, few starvation losses followed this pattern. The preponderance of lynx that died from predation in mature conifer forest is noteworthy because this land cover type was fragmented and comprised only 12% of the study area. Mature conifer was often associated with riparian zones that may have provided resting habitat for lynx (Vashon et al. 2008b), especially during snowfall when hunting efficiency likely decreases. Because mature conifer forest also provides cover and resting sites for fishers (Allen 1983), the use of this land cover type by lynx may increase encounter rates and their vulnerability to predation. In addition, fisher movement is restricted in the deep soft snow of midwinter (Raine 1983). Because the majority of lynx killed by fishers (86%) occurred from January to March when snow was the deepest, fishers may have sought mature conifer forest where snow depth was

lower, further increasing encounter rates. R. D. Weir (personal communication) also noted that it had been snowing when a fisher killed a lynx in British Columbia, Canada.

Powell et al. (2003) observed that fishers surprised their prey in refuges, sometimes after being tracked in the snow, and were only captured if they were overtaken quickly. We theorize that snow provides fishers the added advantage of stealth leading to a successful ambush of a resting lynx. This idea is further supported by limited sign of struggle observed at mortality sites. Our observations of fisher killing and feeding behavior were similar to Powell's (1981) where fishers killed their prey with a bite to the back of the neck or head, cached prey remains in cavities, and often slept close to their prey.

Winter severity in northern Maine also likely played a role in fisher predation of lynx. Winter is a period of food stress for most predators (Halpin and Bissonette 1988, Persson 2005, Zalewski 2005), especially in northern latitudes when potential prey items are less accessible (e.g., hibernating, subnivean). Not only did 86% of fisher predations occur during the winter, but fishers also killed more lynx after 2006, coinciding with lower hare densities (1 hare/ha vs. 2 hares/ha before 2007) in regenerating clear-cuts on our study site (Vashon et al. 2012). Other studies of fishers have demonstrated the importance of alternate prey when hare populations were low (Kuehn 1989, Bowman et al. 2006). Additionally, digestive and metabolic efficiencies are higher for larger prey (e.g., deer carrion, porcupine [*Erethizon dorsatum*]) with a greater ratio of meat than found in smaller prey (Powell 1981). In northern Maine, lynx may have been the most profitable food item for fishers, especially in winter when there were fewer foraging choices and when snowshoe hare densities were lower.

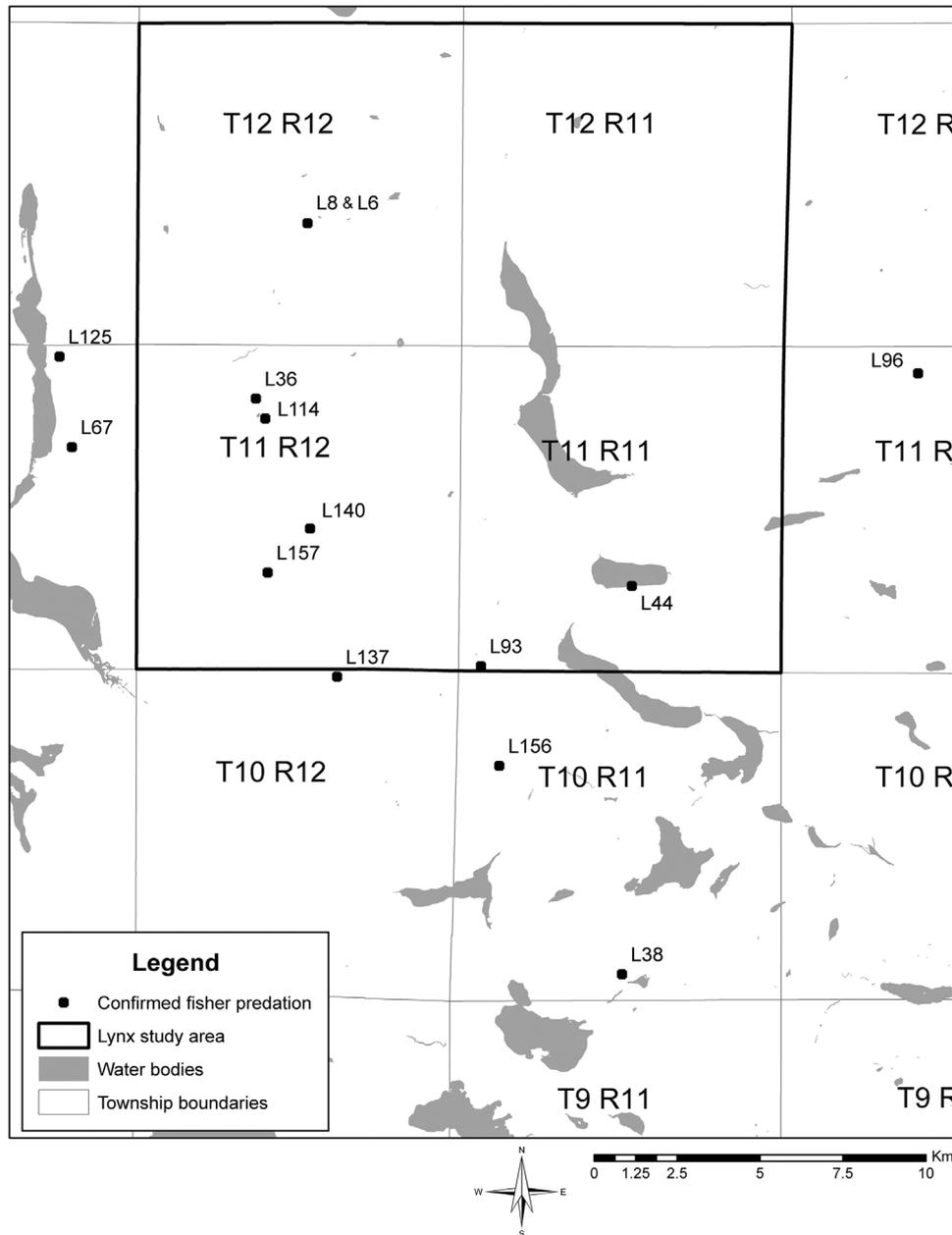
It also seems plausible that fishers would have killed younger, transient lynx, or lynx that were in poor body condition. However, all predation events in this study involved adult lynx with established home ranges, except for an 8-month-old kitten that was killed with its mother. In addition, the examination of femur bone marrow indicated that most lynx were healthy at the time that they were

attacked by a fisher, even during the years of lower snowshoe hare abundance (2007–2011).

It is unlikely that fishers killed lynx in Maine as a result of a specific, learned behavior by 1 or 2 individuals, nor as a result of preying upon weaker individuals. Instead, the spatial and temporal distributions of lynx mortalities (Fig. 2) encompassed the territories of multiple radio-collared fishers over a 12-year period (MDIFW, unpublished data), suggesting that fishers were opportunistic predators of lynx. In addition, during the first 8 years of the study when snowshoe hare densities were  $>1$  hare/ha, only female lynx were killed by fishers, possibly because of their smaller body size. However, when hare densities declined to  $<1$  hare/ha, more lynx were

killed (64%) and both male and female lynx were killed, suggesting that fishers were opportunistically killing what they encountered (Golightly et al. 2006).

Although fishers are not as well adapted as lynx in environments with deep snow because of their shorter legs, they are better adapted to these conditions than other predators in the region that have a higher foot-load (e.g., coyotes; Krohn et al. 2004). The absence of other known predators of lynx (e.g., wolverines, mountain lions, wolves) in northern Maine, along with favorable habitat conditions, may have created a unique opportunity for fishers. Although fishers are smaller and weigh less than lynx ( $\bar{x}=4.6$  kg,  $n=20$ ; MDIFW, unpublished data), they are aggressive



**Figure 2.** The distribution of 14 Canada lynx locations where they were killed by fishers in northern Maine, USA, 1999 and 2011. Predation events are labeled with the lynx identification number and townships are labeled as townships (T) and range (R).

predators, which under the right circumstances can give them an advantage over lynx. Despite the size difference, our data show that fishers are capable of selecting a more profitable prey item in winter (Type III functional response), but there was no information to demonstrate that fishers are competitively excluding lynx from habitats, or are limiting the range or number of lynx in Maine.

## MANAGEMENT IMPLICATIONS

Despite fisher killing lynx in Maine, we have not modified our trapping regulations to increase the harvest of fishers to improve conditions for lynx because Maine's lynx population has been growing in response to abundant habitat and prey (Vashon et al. 2012, USFWS 2017). Conversely, recent trapping regulations for fishers have become more restrictive to minimize the incidental take of lynx. However, these restrictions have limited trapping effort and harvest of fishers. Therefore, predation may be having a greater effect on lynx population dynamics in Maine. Thus, it will be important to continue to monitor these trends and their impacts to inform future management decisions. In areas where lynx and fishers coexist, we recommend that managers consider modifying the harvest of fishers if predation is depressing the population growth rates of lynx. However, continued monitoring of lynx and fishers would be necessary to balance the management and conservation of both species.

## ACKNOWLEDGMENTS

We dedicate this work to the memory of Eric C. York and pilots John "Jack" McPhee and Daryl Gordon, who were all instrumental in the success of this project. Project conception and administrative support of this project was provided by C. R. McLaughlin, J. F. Organ, G. J. Matula, W. J. Jakubas, and C. S. Todd. We thank field technicians J. A. Sikich, S. M. Ritcher, E. C. York, S. M. Mullen, D. E. Perkins, M. Terra-Berns, W. R. Staples, A. J. McCue, J. L. Sika, K. E. Parks, H. M. Shepley, A. P. Jennings, S. A. Boyden, B. C. Nichols, E. M. Rudolph, D. J. Kaminski, C. J. Reynolds, L. J. Perry, J. C. Kuester, L. N. Bates, A. P. K. Siren, D. W. Wagner, T. J. Dorval and volunteers S. M. Mullen, E. J. Pickering, M. D. Pinasci, A. J. McCue, H. M. Shepley, S. S. Schulte, V. A. Crowley, J. J. Haskins, S. A. Boyden, L. M. Shunta, M. Jones, C. S. VanStratt, E. Collins, B. C. Nichols, B. Burkholder, D. J. Kaminski, L. Kehas, K. B. McLellan, K. R. MacCabe, K. Williams, C. M. Vanbianchi, B. S. Coones, M. Nickols, A. J. O'Campo, and J. A. Howard. We thank pilots F. E. Craig, M. Falconeri, C. F. Later, K. Thalinger, and especially D. R. Gordon and J. M. McPhee. We are indebted to Clayton Lake Woodlands and Clayton Lake Woodlands Holdings, LLC for access to their lands and for housing and other logistical support. We are also grateful to J. D. Irving and Orion Timberlands LLC for land access. We appreciate J. A. Webber and M. A. Pokras expertise and diagnostic labs for completing necropsies of lynx during this study. We thank A. L. Meehan for providing GIS expertise. We appreciate the reviews by W. J. Jakubas, J. E. McDonald, J. F. Organ, and S. M. Webb, and the helpful comments of P. J. Pekins. We thank K. S. McKelvey

and 2 anonymous reviewers for constructive comments, which greatly improved this manuscript. Funding for this study was provided by Federal Aid in Wildlife Restoration, Maine State Wildlife Grants, Maine Wildlife Conservation and Restoration Program, and Maine Section 6 Endangered Species Grants. Additional funding was provided by the USFWS Northeast Region Science Support funds, Maine Department of Inland Fisheries and Wildlife, National Council of Air and Stream Improvement, Wildlife Conservation Society, International Paper, National Fish and Wildlife Foundation, Maine Outdoor Heritage Fund, Sweet Water Trust, Defenders of Wildlife, Davis Conservation Foundation, Lynx System Developers, and Plum Creek Foundation.

## LITERATURE CITED

- Allen, A. W. 1983. Habitat suitability index models: fisher. U.S. Fish and Wildlife Service, U.S. Department of the Interior Report FWS/OBS-82/10.45, Washington D.C., USA.
- American Society of Mammalogists. 1998. Guidelines for the safe capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 19:1416–1431.
- Bowman, J., D. Donovan, and R. C. Rosatte. 2006. Numerical response of fishers to synchronous prey dynamics. *Journal of Mammalogy* 87:480–484.
- Bulmer, M. G. 1975. Phase relations in the ten-year cycle. *Journal of Animal Ecology* 44:609–621.
- Buskirk, S. W., L. F. Ruggiero, K. B. Aubry, D. E. Pearson, J. R. Squires, and K. S. McKelvey. 2000. Comparative ecology of lynx in North America. Pages 397–418 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. *Ecology and conservation of lynx in the United States*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Cheatum, E. L. 1949. Bone marrow as an index of malnutrition in deer. *New York Conservationist* 3:19–22.
- Elbroch, M. 2006. *Animal skulls: a guide to North American species*. Stackpole, Mechanicsburg, Pennsylvania, USA.
- Elsy, C. A. 1954. A case of cannibalism in Canada lynx (*Lynx canadensis*). *Journal of Mammalogy* 35:129–129.
- Elton, C., and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology* 11:215–244.
- Fuller, A. K., D. J. Harrison, and J. H. Vashon. 2007. Winter habitat selection by Canada lynx in Maine: prey abundance or accessibility? *Journal of Wildlife Management* 71:1980–1986.
- Golightly, R. T., T. F. Penland, W. J. Zielinski, and J. M. Higley. 2006. Fisher diet in the Klamath/North Coast Bioregion. Department of Wildlife, Humboldt State University, Arcata, California, USA.
- Halpin, M. A., and J. A. Bissonette. 1988. Influence of snow depth on prey availability and habitat use by red fox. *Canadian Journal of Zoology* 66:587–592.
- Homyack, J. A., D. J. Harrison, and W. B. Krohn. 2007. Effects of precommercial thinning on snowshoe hares in Maine. *Journal of Wildlife Management* 71:4–13.
- Keith, L. B. 1963. *Wildlife's ten-year cycle*. University of Wisconsin Press, Madison, USA.
- Koehler, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. *Canadian Journal of Zoology* 68:845–851.
- Krohn, W. B., C. L. Hoving, D. J. Harrison, D. M. Phillips, and H. C. Frost. 2004. Martes foot-loading and snowfall patterns in eastern North America. Pages 115–131 in D. J. Harrison, A. K. Fuller and G. Proulx, editors. *Marten and fishers (Martes) in human-altered environments: an international perspective*. Springer, New York, New York, USA.
- Krohn, W. B., K. D. Elowe, and R. B. Boone. 1995. Relations among fishers, snow, and martens: development and evaluation of two hypotheses. *Forestry Chronicle* 71:97–105.
- Kuehn, D. W. 1989. Winter foods of fishers during a snowshoe hare decline. *Journal of Wildlife Management* 53:688–692.

- O'Donoghue, M., E. Hofer, and F. I. Doyle. 1995. Predator versus predator. *Natural History* 104:6–9.
- O'Donoghue, M., S. Boutin, C. J. Krebs, and E. J. Hofer. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* 80:150–162.
- Olsen, S. J. 2015. Seasonal influence of habitat use by snowshoe hares: implications for Canada lynx in northern Maine. Thesis, University of Maine, Orono, USA.
- Parker, G. R., J. W. Maxwell, and L. D. Morton. 1983. The ecology of the lynx (*Lynx canadensis*) on Cape Breton Island. *Canadian Journal of Zoology* 61:770–786.
- Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Canadian Journal of Zoology* 83:1453–1459.
- Poole, K. G. 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. *Journal of Wildlife Management* 58:608–618.
- Powell, R. A. 1981. Hunting behavior and food requirements of the fisher (*Martes pennanti*). Pages 883–917 in J. A. Chapman and D. Pursley, editors. *Worldwide Furbearer Conference Proceedings*. Worldwide Furbearer Conference, Inc., 3–11 August 1980, Frostburg, Maryland, USA.
- Powell, R. A. 1982. The fisher: life history, ecology, and behavior. University of Minnesota Press, Minneapolis, USA.
- Powell, R. A., S. W. Buskirk, and W. J. Zielinski. 2003. Fisher and marten. Pages 635–649 in G. A. Feldhammer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America*. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Raine, R. M. 1983. Winter habitat use and responses to snow cover of fisher (*Martes pennanti*) and marten (*Martes americana*) in southeastern Manitoba. *Canadian Journal of Zoology*. 61:25–34.
- Scott, S. A. 2009. Spatio-temporal dynamics of snowshoe hare density and relationships to Canada lynx occurrence in northern Maine. Dissertation, University of Maine, Orono, USA.
- Seymour, R. S., and M. L. Hunter, Jr. 1992. New forestry in eastern spruce-fir forests: principals and applications to Maine. Maine Agricultural Experiment Station Miscellaneous Publication 716, Orono, USA.
- Slough, B. J., and G. Mowat. 1996. Lynx population dynamics in an untrapped refugium. *Journal of Wildlife Management* 60:946–961.
- Squires, J. R., and T. Laurion. 2000. Lynx home range and movements in Montana and Wyoming: preliminary results. Pages 337–350 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2000. Endangered and threatened wildlife and plants: determination of threatened status for the contiguous U.S. distinct population segment of the Canada lynx and related rule, final rule. *Federal Register* 65:16052–16086.
- U.S. Fish and Wildlife Service [USFWS]. 2014. Endangered and threatened wildlife and plants: revised designation of critical habitat for the contiguous U.S. distinct population segment of the Canada lynx and revised distinct population segment boundary, final rule. *Federal Register* 79:54782–54846.
- U.S. Fish and Wildlife Service [USFWS]. 2017. Species status assessment for the Canada lynx (*Lynx canadensis*) contiguous U.S. distinct population segment. Version 1.0, October 2017. USFWS, Lakewood, Colorado, USA.
- Vashon, J. H., S. R. McLellan, S. M. Crowley, A. L. Meehan, and K. Laustsen. 2012. Canada lynx assessment. Maine Department of Inland Fisheries and Wildlife, Bangor, USA.
- Vashon, J. H., A. L. Meehan, W. J. Jakubas, J. F. Organ, A. D. Vashon, C. R. McLaughlin, G. J. Matula, and S. M. Crowley. 2008a. Spatial ecology of a Canada lynx population in northern Maine. *Journal of Wildlife Management* 72:1479–1487.
- Vashon, J. H., A. L. Meehan, J. F. Organ, W. J. Jakubas, C. R. McLaughlin, A. D. Vashon, and S. M. Crowley. 2008b. Diurnal habitat relationships of Canada lynx in an intensively managed private forest landscape in northern Maine. *Journal of Wildlife Management* 72:1488–1496.
- Wade, D. A., and J. E. Bowns. 1985. Procedures for evaluating predation on livestock and wildlife. Bulletin Number B-1429. Texas Agricultural Extension Service. Texas A & M University, San Angelo, USA.
- Zalewski, A. 2005. Geographical and seasonal variation in food habits and prey size of European pine martens. Pages 77–98 in D. J. Harrison, A. K. Fuller, and G. Proulx, editors. *Marten and fishers (Martes) in human-altered environments*. Springer, Boston, Massachusetts, USA.
- Zielinski, W. J., N. P. Duncan, E. C. Farmer, R. L. Truex, A. P. Clevenger, and R. H. Barrett. 1999. Diet of fishers (*Martes pennanti*) at the southernmost extent of their range. *Journal of Mammalogy* 80:961–971.

Associate Editor: Kevin McKelvey.