Lynx canadensis (Carnivora: Felidae)

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Abstract: *Lynx canadensis* Kerr, 1792, commonly called the Canada lynx, is a medium size felid and is the second largest of the four species in the genus *Lynx*. It is distributed throughout the boreal forest of most of Canada and Alaska and across portions of the northern United States. It prefers dense, regenerating coniferous forests with moderate canopy and understory cover. *L. canadensis* is a snowshoe hare specialist, and its ecology, morphology, and behavior closely reflect that of its main prey. It is listed as "Least Concern" by the International Union for Conservation of Nature and Natural Resources, is on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora, and its population size trend is considered stable. However, the status of United States subpopulations, being largely peripheral to the Canadian population, is more tenuous and the species is protected.

Key words: Canada lynx, Canadian lynx, carnivore, density cycle, felid, North America

Lynx canadensis Kerr, 1792

Canadian Lynx

F[*elis*]. *Lynx canadensis* Kerr, 1792:157. Type locality "Canada;" restricted to "Eastern Canada [= Quebec]" by Miller (1912:119).

Felis canadensis: É. Geoffroy Saint-Hilaire, 1803:120. Name combination.

Lynx canadensis: Rafinesque, 1817:46. First use of current name combination.

Felis borealis: Temminck, 1824:109. Name combination; part, not *Felis borealis* Thunberg, 1798.

Lynx borealis canadensis: True, 1885:611. Name combination.

Lynx subsolanus Bangs, 1897:49. Type locality "Codroy, Newfoundland."

Lynx canadensis mollipilosus Stone, 1900:48. Type locality "Wainwright Inlet, Pt. Barrow, Alaska."

[*Lynx canadensis*] *subsolanus*: Elliot, 1901:296. Name combination.

Felis (*Lynx*) *lynx canadensis*: Kurtén and Rausch, 1959:44. Name combination.

Fig. 1.—An adult *Lynx canadensis*. Used with permission of Quebec Ministry of Natural Resources.

CONTEXT AND CONTENT. Order Carnivora, suborder Feliformia, family Felidae, subfamily Felinae, genus *Lynx*. *Lynx* currently contains four recognized species (*canadensis*, *lynx*, *pardinus*, and *rufus*—Sunquist and Sunquist 2009; Kitchner 2017); a generic synonymy and key to the species of *Lynx* is provided in Larivière and Walton (1997). Three subspecies were recognized by Wozencraft (2005); however, Sunquist and Sunquist (2009) and Banfield (1974) recognized only two (*canadensis* and *subsolanus*). More recently, *L. canadensis* has been presented as monotypic by Kitchner et al. (2017) who interpreted the level of morphologic and genetic differences between the taxa as insufficient to support subspecific status for *subsolanus* and *mollipilosus*. The following three subspecies are those presented by Wozencraft (2005):

L. c. canadensis Kerr, 1792:157. See above.
L. c. mollipilosus Stone, 1900:48. See above.
L. c. subsolanus Bangs, 1897:49. See above.

NOMENCLATURAL NOTES. Since Kerr's 1792 description of *Lynx canadensis* its taxonomic placement has been questioned. During the 1970s through the 1990s, some researchers (Van Gelder 1977; Corbet 1978; Hemmer 1978; McKenna and Bell 1997; Groves 1982; McCord and Cardoza 1982; Tumlison 1987) thought that either data were insufficient or that differences between species were not great enough to warrant a separate genus and thus retained *Lynx* as a subspecies within *Felis*. Others (Matyushkin 1979; Hall 1981; Werdelin 1981; Garcia-Perea 1992; Wozencraft 1993) supported *Lynx* as a distinct genus. *L. canadensis* has been considered as conspecific with *L. lynx* (Kurtén and Rausch 1959; Weigel 1961; McCord and Cardoza 1982; Quinn and Parker 1987; Tumlison 1987) and as a distinct species (Matyushkin 1979; Kurtén and Anderson 1980; Werdelin 1981; Garcia Perea 1992; Wozencraft 1993). More recently Wozencraft (2005), in his revision of Carnivora, placed *canadensis* under *Lynx* along with *L. lynx*, *L. pardinus*, and *L. rufus* and Kitchner et al. (2017) in a revision of the Felidae presented *L. canadensis* as a monotypic species.

Analyses using 16S rRNA and NADH-5 indicated that *L. canadensis* and *L. lynx* are sister taxa with an older ancestor common to *L. rufus* (Johnson and O'Brien 1997; Pecon-Slattery et al. 2004; Johnson et al. 2006). However, another analysis using a Y chromosome marker recovered a sister relationship between *L. rufus* and *L. lynx* to the exclusion of *L. canadensis* (Pecon-Slattery and O'Brien 1998).

Lynx canadensis previously was described under *Felis lynx* (Tumlison 1987). Other vernacular names include Canada lynx, lynx du Canada (French), loup-cervier (French), pishu (Cree), lucivee, lynx, wildcat, link (Yukon Territory and Interior Alaska), and lynx cat.

DIAGNOSIS

Lynx canadensis (Fig. 1) is the tallest lynx in North America and can be differentiated from the sympatric bobcat *L. rufus* by its larger size (head–body length 76.2–106.7 cm versus 65–105 cm in *L. rufus*—Sunquist and Sunquist 2009), its large, widely spreadable and furry feet (feet are smaller, < 30 cm^2, and pads are naked in *L. rufus*), longer legs (height at shoulder > 46 cm versus < 45 cm for *L. rufus*), longer ear tufts (> 2.5 cm versus < 2.5 cm in *L. rufus*), shorter tail (< 0.5 length of hind foot versus > 0.5 length of hind foot in *L. rufus*) and more imprecise spotting on the belly fur (Parker et al. 1983; Larivière and Walton 1997; Rezendes 1999). On average, *L. canadensis* is heavier (mean body weight, males: 10 kg; females: 8.5 kg) than *L. rufus* (mean body weight, males: 9.6 kg; females: 6.8 kg—Anderson and Lovallo 2003) although the opposite has been noted in some areas (Parker et al. 1983; Buskirk et al. 2000). The tip of the tail of *L. canadensis* is black all around and that of *L. rufus* is black on the dorsal surface only (Larivière and Walton 1997). Pelage of *L. canadensis* typically is more grayish (Werdelin 1981; Sunquist and Sunquist 2002; Anderson and Lovallo 2003; Hansen 2007).

Because of geographic variation across populations and even within a single region, distinguishing the skull of *L. canadensis* from that of *L. rufus* and other felids often requires a combination of generalizations (characters that do not always hold across the entire geographic range) and specific measurements. The skull of *L. canadensis* (Fig. 2) differs from that of *L. rufus* by its typically larger size, relatively smaller auditory bullae, wider interorbital breadth (> 30 mm), larger presphenoid (> 6 mm at its widest portion), typically smaller and more anterior position of the postorbital processes of the frontal bones, longer upper carnassial (> 16 mm), and by the separation of the anterior condyloid foramen from the foramen lacerum (Jackson 1961; Hoffmeister 1989; Elbroch 2006). The skull of *L. canadensis* can typically be differentiated from other felids by the narrower nasal branch of the premaxilla, the thinner, less depressed, and sharper postorbital processes, less deeply notched suborbital margins of the palate, and closeness to the canine and more forward placement of the first large upper premolar (Pocock 1917a).

GENERAL CHARACTERS

Lynx canadensis is a medium-sized (6–14 kg) felid that possesses a round head, short nose, long, pointed ears, long limbs, large feet, and short tail (Sunquist and Sunquist 2002). Pelage is gray to silver-gray, with a blueish tinge in young animals. Summer pelage is darker (Saunders 1964). Some *L. canadensis* have the blue or dilute mutation characterized by bluish-gray replacing black in the pelage (Jones 1923; Schwarz 1938; Denis 1964). White fur occurs on eyelids, inside of ears, chin, throat, and dorsum. The outside fur of the ears is brown with a white central spot and the facial ruff is well developed (Hall 1981). Pads become fully furred in winter (Denis 1964).

Males are larger than females. Mean (except where noted) body mass (kg; *n*, range or *SD*) of *L. canadensis* males and females, respectively, was: 12.53 (7, 9.98–13.15), 10.14 (14, 8.16–11.11) in Alaska (Berrie 1971; Stephenson et al. 1991); 10.55 (5, 9.08–11.80), 8.70 (3, 7.50–9.50) in Alberta (van Zyll de Jong 1975); 15 (single male), 12.3 (2, 10.9, 13.6) in Manitoba

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of *Lynx canadensis* from Quebec (adult male, 5.5 years of age, captured in Baie Comeau on November 1982, mammalogy collection of Laval University Department of Biology). Greatest length of cranium is 123.86 mm.

(Carbyn and Patriquin 1983); 10.9 (7, 9.1–12.2), 9.9 (16, 5.4–12.7) in Michigan (Erickson 1955; Beyer et al. 2001); 10.6 (18, 6.0–13.2), 9.1 (26, 5.9–15.0) in Minnesota (Mech 1977, 1980; Moen et al. 2010); mean not given (83, 4.1–9.0), mean not given (71, 2.2–8.2) in Nova Scotia (Parker et al. 1983); 9.05 (31, ± 1.19), 7.08 (15, ± 1.36) in the Northwest Territories (Murray and Boutin 1991; Poole et al. 1998); 12.3 (1), 8.6 (1) in Wisconsin (Schorger 1947; Doll et al. 1957); 10.7 (93, 6.4–17.3), 8.6 (91, 5.0–11.8) in Nova Scotia (Saunders 1964); and 11.3 (27, range not given), 10.0 (19, range not given) in Yukon (Slough and Mowat 1996; O'Donoghue et al. 1997). Additional body masses (kg) of individual *L. canadensis* were: 15.9 (adult, male) in British Columbia (Poszig et al. 2004); 12.3 (adult, male) in Iowa (Rasmussen 1969); 12.7 (adult, male) in Maine (Fuller 2004); 8.2 (kitten) in November in Manitoba (Carbyn and Patriquin 1983); 10.0 (adult, male), 7.0 (adult, female), 4.0 (juvenile, female) in Montana (Koehler et al. 1979); 15.0 (adult, male), 9.9 (kitten, male), 4.5 (kitten, female) in Wyoming (Blanchard 1959); 7.80 (yearling, female), 3.75 (kitten, male) in January, 3.75 (kitten, female) in January, 5.50 (kitten, female) in April, 6.80 in Yukon (O'Donoghue et al. 1995; Mowat and Slough 1998).

Mean measurements (mm, *n*, range or *SD*) of males and females, respectively, were: total length 1,030 (4, 995–1,050), 980 (7, 950–1,010); length of tail 140 (4, 100–150), 110 (8, 100–140); length of hind foot 250 (4, 230–260), 230 (8, 220–240) in Alaska (Berrie 1971); total length 920 (12, 850–1,050), 860 (11, 780–950); length of tail 110 (12, 100–120), 100 (11, 80–110); length of hind foot 230 (12, 220–250), 220 (11, 210–240) in Alberta (van Zyll de Jong 1975); total length 892.6 (96, 736.6–1,066.8), 844.0 (89, 762.0–965.2); length of tail 104.6 (96, 50.8–127.0), 97.0 (95, 76.2–121.9); length of hind foot 234.2 (95, 203.2–260.4), 223.0 (89, 190.5–247.7) in Newfoundland (Saunders 1964); height at chest 467 (30, ± 10.4), 422 (15, ± 6.3) in the Northwest Territories (Murray and Boutin 1991); total length 852.8 (120, ± 3.21), 812.7 (118, ± 3.00) in Ontario (Quinn and Gardner 1984). Hall (1981) presented the following ranges of measurements (mm, mixed sexes, sample size not specified): total length (825–954), length of tail (95–125), length of hind foot (203–250). Parker et al. (1983) reported the following ranges of measurements (mm) for 83 males and 71 females, respectively, from Nova Scotia: total length 770–950, 740–910; length of hind foot 132–158, 122–148; height at shoulder 430–530, 410–520. Additional measurements (mm) of individual *L. canadensis* were: total length 965.0 (adult, male), length of tail 152 (adult, male), length of hind foot 140 (adult, male) in Iowa (Rasmussen 1969); total length 1,219.2 (adult, male) in Michigan (Erickson 1955); total length 840.0 (adult, female), length of hind foot 220.0 (adult, female), length of ear 65.0 (adult, female), neck circumference 205.0 (adult, female) in Minnesota (Mech 1977); total length 830.0 (adult, female), length of hind foot 211.0 (adult, female), length of tail 90.0 (adult, female), length of ear 62 (adult, female) in Wisconsin (Doll et al. 1957); total length 978.0 (adult, male), length of hind foot 241.0 (adult, male), height of shoulder 603.0 (adult, male), length of ear tuft 48.0 (adult, male) in Wisconsin (Schorger 1947); total length 968.0

(kitten, male), 759.0 (kitten, female), length of tail 127.0 (kitten, male), 86.0 (kitten, female), length of hind foot 260.0 (kitten, male), 221.0 (kitten, female), length of ear 86.0 (kitten, male), 76.0 (kitten, female) in Wyoming (Blanchard 1959).

Mean skull measurements (mm, *n*, range or *SD*) of males and females, respectively, were: greatest length of skull 129 (23, ± 4.10), 122 (13, ± 2.95); basilar length 108 (24, ± 4.01), 101 (13, ± 2.48); zygomatic breadth 94 (24, ± 3.22), 89 (12, ± 1.89); maxillary toothrow 40 (24, ± 1.22), 37 (15, ± 0.86); canine width 35 (22, ± 2.75), 32 (15, ± 0.99) in Newfoundland (Saunders 1964); greatest length of skull130.28 (9, 117.41–135.82), 124.09 (9, 117.60–129.30); condylobasal length 118.02 (125, 104.04–126.48), 112.86 (135, 98.99–126.24); basilar length, 106.62 (1), 102.61 (4, 99.49–105.66); palatilar length 47.56 (9, 41.94–49.54), 45.20 (9, 42.68–47.66); zygomatic breadth 91.84 (11, 83.02–96.50), 87.51 (13, 82.18–91.40); interorbital breadth 29.40 (11, 26.54–32.40), 27.83 (13, 25.83–30.18); braincase breadth 57.92 (10, 55.48–60.30), 56.93 (13, 54.24–58.78); mastoidal breadth 55.21 (10, 49.52–59.04), 53.10 (9, 51.07–55.38); maxillary toothrow 39.69 (2, 39.1, 40.27), 40.46 (4, 39.19–42.90); mandible length 84.90 (10, 76.58–88.24), 81.95 (13, 78.50–87.14—Elbroch 2006). Hall (1981) presented the following ranges of skull measurements (mm, mixed sexes, sample size unknown) greatest length of skull (120–136), zygomatic breadth (82–93), alveolar length of maxillary toothrow (38.1–41.6). In juveniles, the sagittal crest is not developed, the humerus is small (males < 140 mm, females < 125 mm), and the epiphyseal suture is not ossified (Saunders 1964). Foot measurements (*n*, *SD*) of males and females, respectively, were: foot area 286.4 cm^2 (30, ± 28.4), 275.6 cm^2 (15, ± 27.7) and foot-loading: 31.6 g/cm^2 (30, ± 5.2), 25.9 g/cm^2 (15, ± 5.5) for specimens in the Northwest Territories (Murray and Boutin 1991).

DISTRIBUTION

The geographic range of *Lynx canadensis* extends throughout the boreal forests of most of Canada and across the northern parts of the United States (Fig. 3). The northern distribution of *L. canadensis* is limited by tree line in Alaska, Labrador, Northwest Territories, Nunavut, Quebec, and Yukon, whereas it is limited by snowfall and competition with *L. rufus* and the coyote *Canis latrans* in the south (Buskirk et al. 2000; Ruggiero et al. 2000). The northern limit of its range has not changed significantly for at least the past two centuries, but the southern limit has been pushed northward in the Great Plains, Ontario, and Quebec (Poole 2003). In Canada, *L. canadensis* is present in all provinces and territories except Prince Edward Island. It is also absent from mainland Nova Scotia, the Canadian west coast, and the southern Prairie. However, historically, *L. canadensis* occurred in mainland Nova Scotia and Prince Edward Island. In the continental United States, it was formerly found in 24 states and as far south as Utah during the mid-1800s (McKelvey et al. 2000a). Currently, *L. canadensis* only occurs in some southern extensions of boreal forest (McKelvey et al. 2000a; Hoving et al. 2003) in northern Maine, northern Minnesota, western Colorado, Northern Montana, Northern Idaho,

north-central Washington, and north-central Oregon. *L. canadensis* individuals have been sighted in Nebraska, Vermont, and New Hampshire (Hoffman and Genoways 2005; Leon-Kilpatrick 2015). Except for Alaska where it is abundant, the largest populations in the United States are found in Maine and Montana. The occasional appearance of *L. canadensis* in other states probably represents an increase of dispersers from Canada during the peak of abundance (McKelvey et al. 2000a).

FOSSIL RECORD

There are two different hypotheses concerning lynx evolution, one based on fossils and morphology, and a more recent one based on genetics. The hypothesis based on fossils and morphology suggests that the genus *Lynx* probably originated in Africa during the early or mid-Pliocene (Werdelin 1981). The lynx ancestor, *Lynx issiodorensis* migrated into the Northern Hemisphere during the Villafranchian and gave rise to the Eurasian lynx *L. lynx* in Asia (Werdelin 1981). *L. lynx* then spread eastwards in North America giving rise to *L. canadensis* probably during the Sangamonian or the early Wisconsinan (Werdelin 1981).

In contrast, the genetic hypothesis states that the genus *Lynx* probably originated in North America around 6.7 million years ago (Mattern and McLennan 2000; Johnson et al. 2006). A common ancestor to five felid lineages (domestic cat [*Felis*], leopard cat [*Otocolobus* and *Prionailurus*], lynx [*Lynx*], ocelot [*Leopardus*], and puma [*Acinonyx* and *Puma*]) migrated from Asia to North America across the Bering land bridge 8.5–8.0 million years ago (Janczewski et al. 1995; Johnson et al. 2006). This common ancestor gave rise to *L. rufus* 3.24 million years ago and then differentiated into *L. canadensis* and the progenitors of *L. lynx* and the Iberian lynx *L. pardinus* 1.61 million years ago (Johnson et al. 2006).

Lynx canadensis was present in refugia in Beringia and south of the ice edge (Kurtén and Anderson 1980). The oldest fossil, found in the southern refugium, dates from the Sangamonian interglacial, 130,000–115,000 years ago (Kurtén and Anderson 1980). Fossils of *L. canadensis* are reported from the late Pleistocene deposits at Bighill Creek Formation and near Medicine Hat, Alberta (Wilson and Churcher 1984; Harrington 1990), near American Falls, Idaho (Pinsof 1998), near Silver Creek, Utah (Miller 1976), and from the Aftonian deposits near Delight, Washington (Fry and Gustafson 1974). *L. canadensis* started utilizing the snowshoe hare *Lepus americanus* as its main prey probably in the late Pleistocene or early Holocene (Breitenmoser et al. 1993). It probably immigrated to Newfoundland early in the postglacial period (Cameron 1958) but was rare until 1896 (Bergerud 1967).

FORM AND FUNCTION

Form.—Dental formula of *Lynx canadensis* is I 3/3, C 1/1, P 2/2, M 1/1 total of 28, and deciduous dentition formula is I 3/3, C 1/1, P 2/2, M 0/0 total of 24 (Saunders 1964). The
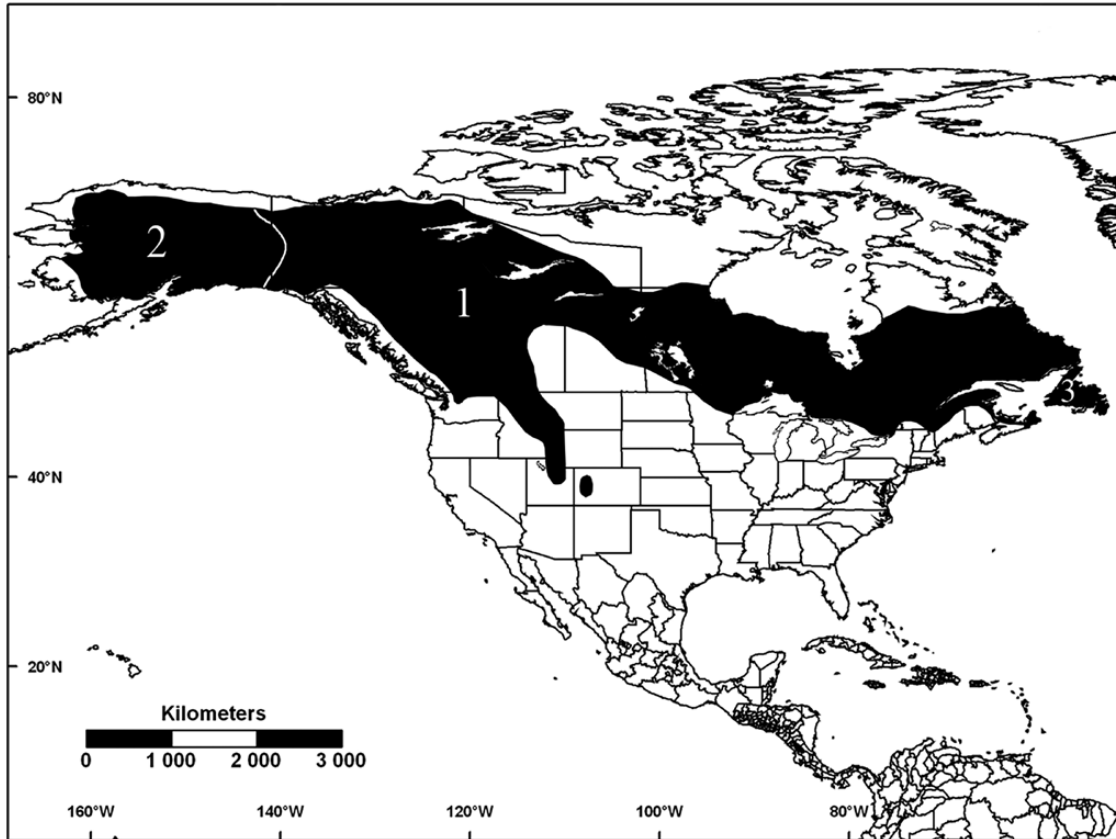
Fig. 3.—Geographic distribution of *Lynx canadensis* in North America. Subspecies are: 1, *L. c. canadensis*; 2, *L. c. mollipilosus*; 3, *L. c. subsolanus*. Map drawn with information from Slough and Mowat (1996), Schwartz et al. (2002), Anderson and Lovallo (2003), Poole (2003), Hoving et al. (2005).

external morphology of the brain, especially the position and shape of the sulci, is different from other species of felids (Radinsky 1975). *L. canadensis* seems to have a rounder and larger brain than most felids and the mean endocast volume of the brain of four specimens is 70 cm³ (Radinsky 1975).

The temporal ridges on the parietal bones have a lyre shape with a width of 72% and 69% of the braincase for males and females, respectively (Saunders 1964). In adults, the temporal ridges join together to form the sagittal crest (Saunders 1964). The sagittal crest and the lambdoidal ridge increase in dimension with age and size, the ossification of the humerus is completed by the end of the second year, and the skeletal growth of males around the 34th month (Saunders 1964). The auditory bulla is broader in the anterior portion of the inner chamber and narrower in its posterior portion compared to that of *L. lynx* (Pocock 1916).

Lynx canadensis is digitigrade with sharp, retractile claws. Front and hind feet have four functional toes. The plantar pad of the front foot is short compared to its width and the claw sheaths are well developed. Toes are united by a deep web (Pocock 1917b).

Female *L. canadensis* have four mammae (two inguinal and two abdominal) and males have a small baculum. Bregmatic bones occur rarely (1/472 and 0/617 museum specimens examined—Pratt 1942; Manville 1959).

Function.—Basal metabolism in *Lynx canadensis* is similar in winter and summer (Casey et al. 1979). *L. canadensis* maintains its body temperature at 38.8°C and increases its respiratory frequency in response to increasing temperature ranging from 20 respirations per minute at −20°C to 30 respirations per minute at 20°C (Casey et al. 1979). Males have higher concentrations of fecal glucocorticoid metabolites at the onset of the breeding season, whereas the increase occurs toward the end of the breeding season for females (Fanson et al. 2012).

The webbing uniting the toes helps *L. canadensis* walk on snow (Pocock 1917b). Males and females have similar mean foot-loads (ratio of body mass to foot area) but yearlings have a lower foot-load than adults (Murray and Boutin 1991). The large paws, long limbs, and low foot-load of *L. canadensis* likely provide an advantage for travel in deep snow compared to other predators which have smaller limbs and paws (Koehler and Brittell 1990; Murray and Boutin 1991; Buskirk et al. 2000). *L. canadensis* has both long legs and low foot-loading (Buskirk et al. 2000). Snow hardness affects sinking depth of lynx but not snow depth and *L. canadensis* sinks on average 7.7 cm in snow (Murray and Boutin 1991). One male *L. canadensis* penetrated from 9 to 14 cm in snow (Poszig et al. 2004).

Yearlings have lower body fat than adults (Brand and Keith 1979; Parker et al. 1983). Females have less subcutaneous fat than males and yearlings have less renal fat than adults because of the higher energy requirement during growth (Brand and Keith 1979). Renal and subcutaneous fat seem to be affected only by snowshoe hare abundance during late winter (Brand and Keith 1979). Fat reserves generally decline from November to January and increase from January to February (Parker et al. 1983). Blood parameters of *L. canadensis* are available (Weaver and Johnson 1995).

Evidences from captive *L. canadensis* showed that olfaction might be poorly developed but auditory and visual senses are good (Saunders 1963a). *L. canadensis* has a solid mandibular symphysis allowing it to cut flesh proficiently (Scapino 1981).

ONTOGENY AND REPRODUCTION

Ontogeny.—Kittens of *Lynx canadensis* are born reddish-brown with stripes and spots (Merriam 1886; Denis 1964); newborns have eyes closed, no teeth, poorly developed ear tufts, ears folded forward, but pelage well developed with guard hairs and underhairs (Saunders 1964). The pelage of newborn kittens has longitudinal streaks more apparent on the back than the flanks, with dark horizontal bars on the front legs (Merriam 1886; Saunders 1964). Eyes open after 10 days (Denis 1964). Mass of three newborns was 175 g (Slough and Mowat 1996), 197 g, and 211 g (Saunders 1964). Kittens gain 5–8 kg during the first 300 days of life and may double their weight within 300 days (Moen et al. 2010). Lengths of two neonates were 163 and 158 mm (Saunders 1964).

Lynx canadensis often gives birth and rears young in different dens (Slough 1999; Squires et al. 2008). Female *L. canadensis* use dens from birth until the kittens are foraging at about 6–8 weeks old (Slough 1999) and decrease their movements while denning (Moen et al. 2008). Kittens usually stay close to their dens the first 7 days after parturition and start gradually following their mother further away until they reach their mother's predenning movements around 50 days after parturition (Moen et al. 2008). They can hunt by themselves by the spring following their birth (Brand et al. 1976).

Lynx canadensis reaches adult size during its second year (Saunders 1964; Parker et al. 1983). The environment during the growing period is important for adult body size (Yom-Tov et al. 2007). *L. canadensis* reaches sexual maturity sooner during high snowshoe hare densities (Brand et al. 1976; Parker et al. 1983). Female *L. canadensis* can conceive during their first year at about 9–10 months of age but usually do not give birth before their second breeding season (Brand et al. 1976; Parker et al. 1983; Breitenmoser et al. 1993; Moen et al. 2008). Male *L. canadensis* generally do not breed before their second year and gametogenesis is reduced during summer and autumn (Anderson and Lovallo 2003).

Reproduction.—*Lynx canadensis* is capable of ovulating spontaneously but female ovarian activity increases between

February and April (Fanson et al. 2010). Breeding occurs in March and April (Saunders 1964; Poole 1994) but may take place as late as May in Alberta (Nellis et al. 1972). Pair bonds are short, and males do not provide parental care.

Pregnancy rate ranges from 30% to 100% (Brand and Keith 1979; Quinn and Thompson 1987; Slough and Mowat 1996; Vashon et al. 2012). Productivity of *L. canadensis* is directly linked to snowshoe hare numbers (Nellis et al. 1972), with larger litters observed in years of higher snowshoe hare density (Brand and Keith 1979; Slough and Mowat 1996). At all densities, adult females produce higher litter size and have higher pregnancy rates than do yearlings (Parker et al. 1983; Mowat et al. 1996a). Females can have one litter per year but during low snowshoe hare densities, interbirth intervals may be 2 years (Anderson and Lovallo 2003). In the Yukon, adult females reproduced each year except the second and third years following snowshoe hare decline. In contrast, yearling females reproduced only during years of high snowshoe hare density (Slough and Mowat 1996). Similarly, in Alberta, 73% of adult females gave birth in years of high snowshoe hare abundance compared to 33% in snowshoe hare scarcity (Brand and Keith 1979).

Gestation lasts 61–70 days (Denis 1964; Hemmer 1976). Young are born in late May to early June (Saunders 1964; Slough 1999) but *L. canadensis* can give birth 6 weeks later than normal during years when snowshoe hare abundance is elevated (Mowat and Slough 1998). Litter size ranges from 1 to 8 (Nellis et al. 1972; Brand et al. 1976; Mowat and Slough 1998; Moen et al. 2008). Corpora lutea persist for more than one breeding season (Nellis et al. 1972).

ECOLOGY

Population characteristics.—*Lynx canadensis* is a snowshoe hare specialist, and its ecology, morphology, and behavior reflect closely that of its main prey (O'Donoghue et al. 1998a, 1998b). Mortality is higher during winter (Poole 1994), especially the first winter of low snowshoe hare density (Poole 1994; Slough and Mowat 1996) and death from starvation often coincided with temperatures below −35°C (Poole 1994) during this period of decreased snowshoe hare density. It can survive through two 10-year density cycle peaks (Breitenmoser et al. 1993). In some areas *L. canadensis* cycles may be affected by disease (Gilpin 1973; but see Finerty 1979 and Vik et al. 2008), or intrinsic self-regulation factors (Zhibin et al. 2007).

Lynx canadensis can be killed by coyote (O'Donoghue et al. 1995), wolverine *Gulo gulo* (O'Donoghue et al. 1995; Slough and Mowat 1996), wolf *Canis lupus* (O'Donoghue et al. 1995), mountain lion *Puma concolor* (Koehler et al. 1979), and fisher *Pekania pennanti* (Vashon et al. 2012). Collision with vehicles can also be a significant cause of mortality (Kloor 1999; Steury and Murray 2004) and is an important factor in reintroduction failure (Aubry et al. 2000). *L. canadensis* may also die from cannibalism (Elsey 1954; O'Donoghue et al. 1995; Poole 1997). The oldest *L. canadensis* in captivity died at 26.9 years of age

(Rich 1983) and it can live up to 16 years in the wild (Kolbe and Squires 2006).

Lynx canadensis is highly susceptible to trapping (Mech 1980; Carbyn and Patriquin 1983; Parker et al. 1983; Bailey et al. 1986; Quinn and Thompson 1987), particularly males (Quinn and Thompson 1987). Furthermore, *L. canadensis* may be more vulnerable to trapping during periods when snowshoe hare density is low (Brand et al. 1976). Trapping mortality, where trapping is legal, seems density dependent (Brand and Keith 1979) and is thought to be additive rather than compensatory (Bailey et al. 1986; Quinn and Thompson 1987; Slough and Mowat 1996), especially during high and declining snowshoe hare densities (Poole 1994). However, during the first two winters of low snowshoe hare density, trapping may be partly compensatory (Ward and Krebs 1985; Poole 1994). Slough and Mowat (1996) proposed that local extinctions of *L. canadensis* populations may be prevented by establishing a system of untrapped versus trapped areas. These untrapped areas would allow *L. canadensis* populations to respond more naturally to decreasing snowshoe hare densities.

Lynx canadensis populations undergo density cycles (Krebs et al. 1995). Cycles have been detected in more than 200 years of fur sales from the Hudson's Bay Company (Elton and Nicholson 1942). It follows a periodicity between 9 and 11 years (Brand et al. 1976; Krebs et al. 1995; Korpimäki and Krebs 1996; Ranta et al. 1997) with an average of 9.6 years (Elton and Nicholson 1942). The interval between two lynx cycles is more constant than the amplitude of each cycle (Moran 1953a; Bulmer 1974). Across Canada, the cycle in density is not geographically synchronous but can be separated into three regions: the Atlantic, the Continental, and the Pacific (Stenseth et al. 2004a). These regions match the three climatic-based geographic regions (Stenseth et al. 1999) and the border between the Atlantic and the Continental region is correlated with the geographic pattern of warm spells (Stenseth et al. 2004b). The cycle reaches its peak first in the central provinces (Saskatchewan and Manitoba), then 1 year later in the western provinces (British Columbia and Alberta) and 2 years later in the eastern provinces (Ontario and Quebec—Butler 1953). The cycle may be synchronized by *L. canadensis* dispersal patterns (Butler 1953; Lack 1954). The cycle is caused by a high postnatal mortality, reduced reproduction rates among yearlings (Nellis et al. 1972; Brand and Keith 1979; Parker et al. 1983), and changes in recruitment (Stuart-Smith and Boutin 1995), combined with high adult mortality (Brand and Keith 1979).

Autoregressive (Tong 1977), fixed frequency (Moran 1953a), and a combination of both models (Bhansali 1979) have been used to analyze *L. canadensis* data, to explain the cyclic fluctuation in mathematical terms. Autoregressive models can describe random changes in frequency, phase, or amplitude of oscillations, whereas fixed frequency models assume a fixed predetermined period. Several models have been tested such as using (1) the logarithms of the total animals trapped to reduce both the degree of asymmetry of the oscillations in the original data and the effect of ignoring the fact that the real population abundance is not exactly proportional to the number of animals caught (Moran 1953a), (2) a pure Autoregressive model of order 11 without a fixed component (Tong 1977), (3) a pure sine wave of a period of 9.63 years superposed with a first-order (Bulmer 1974) or (4) second-order Autoregressive process (Campbell and Walker 1977), (5) an Autoregressive model of order 2 combined with a sine wave of a period of 9.5 years (Bhansali 1979), (6) a self-exciting threshold Autoregressive model, that allows more flexibility in model parameters by switching from one regime to another when a threshold is reached, with two regimes of order 7 and 2 (Lai 1996) or (7) with two regimes of order 2 (Stenseth et al. 1998). The previously mentioned models assumed the oscillations to be an autonomous phenomenon and external factors as perturbations only. Other models describe the oscillations as being generated by external factors. Examples of these models follow: (1) a stepwise multiple regression analysis including precipitation in May and temperature in June, September, and October (Arditi 1979), (2) a three-dimensional phase portrait with a deterministic period of 20 years with noise superimposed (Schaffer 1984), (3) a model incorporating plant–herbivore and prey–predator interactions as density ratios (Akçakaya 1992), (4) a bivariate time-series model fitted to snowshoe hare and *L. canadensis* data to consider within- and between-population interactions (Vik et al. 2008), and (5) a uniform phase evolution and chaotic amplitude model to evaluate the presence of a bifurcation process caused by increase trapping pressure or alternative prey (Gamarra and Solé 2000).

The *L. canadensis* density cycle is primarily induced by fluctuations in snowshoe hare density (Butler 1953; Stenseth et al. 1997; Vik et al. 2008) and usually follows 1 or 2 years behind the snowshoe hare cycle (Bulmer 1974; Brand et al. 1976; Boutin et al. 1995; O'Donoghue et al. 1997). Between the low and peak abundance periods for snowshoe hare, *L. canadensis* density increased from 7.5 to 17 times in the Yukon (Boutin et al. 1995; Slough and Mowat 1996; O'Donoghue et al. 1997) and 10 times in the Northwest Territories (Poole 1994). The speed and magnitude of *L. canadensis* recovery from low snowshoe hare densities depends on the number of *L. canadensis* that survive the years of snowshoe hare scarcity (Brand and Keith 1979). The *L. canadensis* cycle is more obvious in northern environments but is still apparent in the southern portion of its geographic distribution, likely due to dispersal of northern individuals (McKelvey et al. 2000b). *L. canadensis* dynamics might differ in populations in southern latitudes because fluctuation in snowshoe hares is more stable than in the north (Koehler 1990) because alternate preys are more abundant (Roth et al. 2007).

The cycle in *L. canadensis* also may be influenced by weather (Moran 1953b; Arditi 1979; Stenseth et al. 1999; Yan et al. 2013). Sunspot numbers are not correlated with the *L. canadensis* cycle (Moran 1949) but solar activity could indirectly, through the effects of the climate cycle on the ecosystem, modulate the snowshoe hare cycle and thus the *L. canadensis* cycle (Sinclair et al. 1993). Forest fire, through plant succession favoring snowshoe hares (Fox and Bryant 1984; Trostel et al. 1987; Krebs et al. 1995), and snowfall may also cause oscillation in *L. canadensis*

densities (Fox 1978). Finally, climate can affect *L. canadensis* population cycles by the relationship of foot-loading to snowfall, by affecting snowshoe hare, and by affecting forest composition (Hoving et al. 2003). However, it has not been shown that *L. canadensis* cycles result from cycle in fur prices (de Vos and Matel 1952; Gamarra and Solé 2000) that modulate trapper harvest effort (Gilpin 1973; Weinstein 1977). The southern range of *L. canadensis* appears to have contracted during the last decade (Bayne et al. 2008) and it has been suggested that climate change may have a negative impact on the distribution of *L. canadensis* populations (Carroll 2007; Bayne et al. 2008).

Age and sex ratios of the harvest data usually differ from the population data and will change seasonally and dependently of the cycle (Quinn and Thompson 1985). Yearlings are overrepresented in harvest, especially in autumn and winter, while kittens are underrepresented but increased after December, when they become more independent (Slough and Mowat 1996). Among yearlings, males are more vulnerable to trapping due to their higher mobility (Saunders 1963a; Mech 1980; Quinn and Thompson 1987). Sex and age ratios of the harvest vary with the cycle, with kittens being absent during the decline and numerous during the peak (Nellis et al. 1972; Brand et al. 1976; Brand and Keith 1979; Poole 1994). Most studies of harvested populations have observed sex bias toward males (Quinn and Gardner 1984), but an even sex ratio or a bias toward females have also been observed (Brand and Keith 1979; Bailey et al. 1986; Quinn and Thompson 1987). It seems that during peak densities in *L. canadensis* populations, males are predominant and during low densities, females are predominant (Poole 1994). Through the cycle, sex ratios usually do not significantly differ from equality (Parker et al. 1983; Poole 1994; Slough and Mowat 1996). Sex ratios (males:females; *n* in parenthesis) were: for kittens 50:50 (8), for yearlings 33:67 (15), and for adults 0:100 (7) in Minnesota (Mech 1980); 57:43 (58) in the Northwest Territories (Poole 1994); for kittens 69:31 (16), for yearlings 57:43 (70), and for adults 50:50 (60) in Nova Scotia (Parker et al. 1983); for kittens 52:48 (178), for yearlings 62:38 (484), and for adults 54:46 (314) in Ontario (Quinn and Thompson 1987); for kittens 51:49 (158), for yearlings 65:35 (401), and for adults 49:51 (329) in Yukon (Slough and Mowat 1996).

During snowshoe hare scarcity, age distribution of *L. canadensis* shifts toward an older cohort due to a lower recruitment (Brand and Keith 1979; Slough and Mowat 1996). The main cause of the decrease in recruitment is kitten mortality ranging from 40% to 100% (Brand et al. 1976; Poole 1994; Mowat et al. 1996b). During periods when snowshoe hare density is low, *L. canadensis* either does not conceive or aborts litters (Mowat and Slough 1998) and survivorship of kittens of yearling females is lower than that of kittens of adult females (Mowat et al. 1996b; Slough and Mowat 1996). When snowshoe hares are abundant, late born kittens can survive winter (Mowat and Slough 1998).

Lynx canadensis densities vary greatly during a snowshoe hare cycle ranging from 2.0 to 44.9/100 km². Densities were 20/100 km² during periods of high snowshoe hare density in Alaska (Bailey et al. 1986), 2–10/100 km² in Alberta (Nellis et al. 1972; Brand et al. 1976), 9.2–13.0/100 km² during a *L. canadensis* peak in Maine (Vashon et al. 2008a), 3.9–7.8/100 km² in Newfoundland (Bergerud 1971), 3–30/100 km² in the Northwest Territories (Poole 1994), 20/100 km² during periods of high snowshoe hare density in Nova Scotia (Parker et al. 1983), 5.9–14.5/100 km² in Quebec (in Slough and Mowat 1996), 2.3/100 km² during periods of low snowshoe hare density in Washington (Koehler 1990), and 2.0–44.9/100 km² in Yukon (Slough and Mowat 1996; O'Donoghue et al. 1997; Boonstra et al. 1998). *L. canadensis* density may be limited in the southern portion of its distribution where the snowshoe hare is restricted by habitat availability (Koehler 1990), thus its densities are typically higher in the north portion of its distribution (O'Donoghue et al. 1997).

Space use.—*Lynx canadensis* occupies habitats where snowshoe hares are abundant (Parker et al. 1983; Koehler 1990; Poole et al. 1996; O'Donoghue et al. 1998a; Hoving et al. 2005; Bayne et al. 2008). Usually, *L. canadensis* occurs in dense coniferous forests with moderate canopy and understory cover, and elevation between 1,525 and 1,829 m but can live at elevations up to 2,400 m (Koehler et al. 1979; Koehler and Brittell 1990; Paragi et al. 1997; Mowat and Slough 2003; Koehler et al. 2008). It avoids deciduous forests, open habitat, steep slopes, and recent burns (Murray et al. 1994; Hoving et al. 2005; Koehler et al. 2008; Vashon et al. 2008b). *L. canadensis* also selects early and late successional habitat like 15- to 30-year-old burns or 15- to 25-year-old forests regenerating from clear cutting and tends to avoid recent clear-cuts and partial harvests (Koehler et al. 1979; Parker et al. 1983; Thompson 1988; Poole et al. 1996; Paragi et al. 1997; Mowat and Slough 2003; Hoving et al. 2004). Mature forest is used for denning, travel corridors, cover, socialization, or to seek alternate prey (Koehler 1990; Paragi et al. 1997; O'Donoghue et al. 1998a) but it will also den in young forest if that is the densest cover available (Organ et al. 2008). Deep snow areas are also important to *L. canadensis* probably because snowshoe hares prefer these areas and competition with other predators is diminished (Murray and Boutin 1991; Hoving et al. 2005). *L. canadensis* is more selective in its habitat use in winter than summer, or when snowshoe hares are scarce (Poole et al. 1996; Mowat et al. 2000; Mowat and Slough 2003).

Lynx canadensis natal and maternal dens are usually fairly close together (Squires et al. 2008), distances range from 107 to 2,700 m (Moen et al. 2008; Organ et al. 2008; Olson et al. 2011). Maternal dens typically occur in coarse woody debris, deadfalls or wind-thrown trees, boulder fields, slash piles, and live trees (Koehler 1990; Slough 1999; Gilbert and Pierce 2005; Organ et al. 2008; Squires et al. 2008). In Montana, dens were usually located on northeastern slopes averaging 24°, in concave or drainage-like areas, had higher horizontal cover and log volume than the surrounding area, abundant woody debris, and were away from forest edges (Squires et al. 2008). *L. canadensis* prefers habitat with less than 5 m visibility for denning (Organ et al. 2008). Den chambers are usually lined with forest litter

and needles and average 80 cm width, 71 cm depth, and 45 cm height (Squires et al. 2008). Relocation of dens may be common (Slough 1999) but each den is usually used only once (Slough 1999; Squires et al. 2008). Dens of neighboring females or dens used the following year can be as close as 300 m (Slough 1999). *L. canadensis* may use caves for rest (Saunders 1963a).

Home range size is correlated with snowshoe hare densities but not in a linear pattern (Brand et al. 1976; Slough and Mowat 1996; Mowat et al. 2000). Home ranges increase during the second year of snowshoe hare decline (Slough and Mowat 1996) or during the first full year of snowshoe hare scarcity (Poole 1994). At the end of the first winter of low snowshoe hare densities, *L. canadensis* either disperses or dies if its home range does not encompass a prey refugium (Poole 1994, 1995, 1997). A resident *L. canadensis* maintain its home range year to year (Koehler et al. 1979; Poole 1995); however, a threshold below which prey densities cannot support any size of home range has been estimated at 0.5 snowshoe hare/ha and this results in *L. canadensis* becoming nomadic (Ward and Krebs 1985).

Lynx canadensis home ranges may also vary according to sex, season, topography, and age. Home ranges of males are generally larger than females (Mech 1980; Parker et al. 1983; Vashon et al. 2008b) and males may select mature conifer more than females because they travel more (Vashon et al. 2008b). Home ranges are usually larger in winter than in summer (Parker et al. 1983; Burdett et al. 2007) because male *L. canadensis* travel more during the breeding season (Vashon et al. 2008a) and females decrease their movements during parturition (Burdett et al. 2007). The shape of home ranges is influenced by topography (Saunders 1963a). In Newfoundland, the home range of an individual coincided almost exactly with a band of 10–20 years old growth timber (Saunders 1963a). Females tend to select areas with higher densities of snowshoe hares (Vashon et al. 2012), and those with kittens tend to have smaller home ranges than adults travelling alone (Saunders 1963a; Brand et al. 1976) and yearlings have less home range fidelity (Quinn and Thompson 1985). Overlapping home ranges occur more frequently with females but males usually exclude other males, especially in the core area (Nellis et al. 1972; Brand et al. 1976; Vashon et al. 2008a). Home range overlap between sexes may be common (Ward and Krebs 1985; Poole 1995) or rare (Mech 1980; Carbyn and Patriquin 1983).

Home ranges of males and females average about 150 and 75 km^2, respectively (Aubry et al. 2000). Average home range size (km^2; *n* in parenthesis) for adult males and females, respectively, were: 423.5 (2), 69.5 (2) in Alaska (Bailey et al. 1986); 145–243 (8), 17–122 (12) in Minnesota (Mech 1980; Burdett et al. 2007); 19.4 (2), 15.5 (1) in Newfoundland (Saunders 1963a); 25.4 (30), 24.4 (24) in the Northwest Territories (Poole 1994); 18.6 (1) and 12.3 (1) in summer, 32.3 (1) and 25.6 (1) in winter in Nova Scotia (Parker et al. 1983); 53.6 (11), 25.7 (11) in Maine (Vashon et al. 2008a); 69 (5), 39 (2) in Washington (Koehler 1990); 60.0 (46), 54.0 (51) in the Yukon (Slough and Mowat 1996). A single male in Montana had a home range of 36 km^2 (Koehler et al. 1979). Home range core areas in km^2 (*n*) for

adult males and adult females, respectively, were: 17.3 (11), 5.3 (11) in Maine (Vashon et al. 2008a); 37 (4), 5 (2) in Minnesota (Burdett et al. 2007); 6.6 (1), 5.3 (1) in Nova Scotia (Parker et al. 1983).

Daily movements of male *L. canadensis* are greater than those of females (Saunders 1963a; Mech 1980). Daily movements (km; ranges or means) for males and females, respectively, were: 3.8 and 3.0 in British Columbia (Apps 2000), 3.8 and 3.8 in Manitoba (Carbyn and Patriquin 1983), 2.5–3.3 and 2.5–3.9 in Montana (Squires and Laurion 2000), 2.0–3.3 and 1.4–2.7 in the Northwest Territories (Poole 1994), 8.8 and 7.6 in Nova Scotia (Parker et al. 1983), 0.7–9.5 and 0.3–5.3 in Wyoming (Squires and Laurion 2000). *L. canadensis* travels on average for 99 min (ranging from 11 to 274 min) at an average speed of 1.09 km/h (ranging from 0.75 to 1.46 km/h) and this rate does not differ between low and high snowshoe hare densities (O'Donoghue et al. 1998b). Daily movements of *L. canadensis* are typically greater in summer than in winter (Parker et al. 1983), though movement increases when snowshoe hare densities are low (Ward and Krebs 1985; Poole 1994). Daily movements increased from 2.2 to 5.5 km in the Yukon (Ward and Krebs 1985) and from 3.0 to 8.9 in Alberta (Nellis and Keith 1968; Brand et al. 1976) when snowshoe hare densities decreased.

Dispersal increases during periods of snowshoe hare decline (Slough and Mowat 1996; O'Donoghue et al. 1997). There is no difference in dispersal distance between sexes, age classes, or resident status (Mech 1980; Slough and Mowat 1996; Poole 1997). Dispersal occurs mainly during March through June and rarely in September and October (Slough and Mowat 1996). During increasing *L. canadensis* populations, immigration is greater than emigration (Slough and Mowat 1996). Dispersal distance ranged up to 103 km in Newfoundland (Saunders 1963a), and 1,100 km in Yukon (Slough and Mowat 1996). The longest recorded dispersals for *L. canadensis* are 164 km in Alberta (Nellis and Wetmore 1969), 403 km in Maine (Vashon et al. 2012), 483 km in Minnesota (Mech 1977), 930 km in the Northwest Territories (Poole 1997), and 1,100 km in the Yukon (Slough and Mowat 1996). During dispersal, daily travel of *L. canadensis* varies from 0.3 to 23.6 km (Slough and Mowat 1996; Poole 1997). Highways might be a barrier to movement for *L. canadensis* (Alexander and Waters 2000).

Diet.—*Lynx canadensis* is a strict carnivore. Throughout its range, diet is comprised from 35% to 100% of snowshoe hares (Brand and Keith 1979; O'Donoghue et al. 1998a). Snowshoe hares compose 35–99% of *L. canadensis* diet in Alberta (Nellis and Keith 1968; Nellis et al. 1972; Brand et al. 1976; Brand and Keith 1979), 89% in Maine (Vashon et al. 2012), 96% in Montana (Squires and Ruggiero 2007), 73% in Newfoundland (Saunders 1963b), 52–83% in the Northwest Territories (van Zyll de Jong 1966a; More 1976), 97% in Nova Scotia (Parker et al. 1983), 79% in Washington (Koehler 1990), and 38–100% in the Yukon (Murray et al. 1994; O'Donoghue et al. 1998b). *L. canadensis* depends more on snowshoe hares during the winter than summer (Saunders 1963b; van Zyll de Jong 1966a; Nellis et al. 1972) and shifts to alternate prey during the

snowshoe hare decline (Brand et al. 1976; O'Donoghue et al. 1998b) or during the summer months in the southern portions of its distribution (Vashon et al. 2012).

The two main alternate prey eaten by *L. canadensis* are ruffed grouse (*Bonasa umbellus*) and red squirrel (*Tamiasciurus hudsonicus*—van Zyll de Jong 1966a; O'Donoghue et al. 1998b; Vashon et al. 2012). Other mammalian prey may include squirrels (*Glaucomys sabrinus*—northern flying squirrel, *Spermophilus columbianus*—Columbian ground squirrel, *Spermophilus parryii*—Arctic ground squirrel, *Spermophilus richardsonii*—Richardson's ground squirrel), mice (*Peromyscus maniculatus*—North American deermouse, *Zapus hudsonius*—meadow jumping mouse), shrews (*Sorex cinereus*—cinereus shrew), and voles (*Microtus pennsylvanicus*—meadow vole, *Myodes gapperi*—southern red-backed vole—van Zyll de Jong 1966a; Nellis et al. 1972; O'Donoghue et al. 1998b). Larger rodents such as muskrat (*Ondatra zibethicus*), beaver (*Castor canadensis*), and porcupine (*Erethizon dorsatum*) also may be consumed (Saunders 1963b; Brand et al. 1979).

Additional species of birds such as grouse (*Canachites canadensis*—spruce grouse, *Dendragapus obscurus*—dusky grouse, *Pedioecetes phasianellus*—sharp-tailed grouse), fox sparrow (*Passerella iliaca*), chickadees (*Poecile*), grey partridge (*Perdix perdix*), ducks (*Anas carolinensis*—green-winged teal, *Anas platyrhynchos*—mallard, *Anas rubripes*—American black duck), willow ptarmigan (*Lagopus lagopus*), northern flicker (*Colaptes auratus*) also may be eaten (Saunders 1963b; van Zyll de Jong 1966a; Nellis and Keith 1968; Squires and Ruggiero 2007).

Lynx canadensis may prey on white-tailed deer (*Odocoileus virginianus*—Parker et al. 1983; Fuller 2004; Squires and Ruggiero 2007), reindeer (*Rangifer tarandus*—Saunders 1963b; Bergerud 1971; Stephenson et al. 1991), Dall's sheep (*Ovis dalli*—Stephenson et al. 1991), and mule deer (*Odocoileus hemionus*—Poszig et al. 2004). On occasion, *L. canadensis* may kill and eat other carnivores such as red fox (*Vulpes vulpes*—Stephenson et al. 1991; O'Donoghue et al. 1998b), American marten (*Martes americana*—Apps 2000), ermine (*Mustela erminea*—O'Donoghue et al. 1998b), and least weasel (*Mustela nivalis*—Squires and Ruggiero 2007). It may also kill domestic animals such as domestic cats (*Felis silvestris catus*—Nellis et al. 1972), domestic cows (*Bos taurus*—Saunders 1963b), red sheep (*Ovis aries*—Saunders 1963b), chickens (*Gallus gallus*—Mech 1973; Mowat and Slough 1998), goats (*Capra hircus*—Mowat and Slough 1998), and domestic dogs (*Canis familiaris*—Mech 1973; Mowat and Slough 1998). *L. canadensis* may eat carrion (Nellis and Keith 1968; Parker et al. 1983; Murray et al. 1994). Other food includes insects (Saunders 1963b).

Lynx canadensis needs 0.4 snowshoe hares per day to meet its daily metabolic requirements (Nellis et al. 1972). Food requirements have been estimated to be 600 g per day for adults, 400 g for juveniles in winter (Nellis et al. 1972), and 620 g per day for captive adults (Saunders 1963b). Consumption rates vary according to prey availability and were evaluated for snowshoe hares and range from 320 g per day during periods of low snowshoe hare density to 960 g per day during high snowshoe hare density (Brand et al. 1976). *L. canadensis* eats about 0.2–0.8 snowshoe hares per day in Alberta (Nellis and Keith 1968; Brand et al. 1976), between 0.47 and 0.56 snowshoe hares per day in Newfoundland (Saunders 1963b), about one snowshoe hare per day in Nova Scotia (Parker et al. 1983), and between 0.3 and 1.2 snowshoe hares per day in the Yukon (O'Donoghue et al. 1998b). The shift to alternate prey during periods of snowshoe hare decline does not compensate for the decrease in biomass of snowshoe hares killed and thus lynx consume 37% less in biomass (Brand et al. 1976).

Diseases and parasites.—In a free-ranging situation, *Lynx canadensis* appears to rarely encounter common feline pathogens or infectious diseases (Biek et al. 2002). Nevertheless, adults can be infected by *Salmonella arizonae* (Macri et al. 1997), feline coronavirus, canine distemper virus, feline calcivirus, feline herpesvirus, *Francisella tularensis*, *Yersinia pestis*, oral papillomatosis (Wild et al. 2006; Wolfe and Spraker 2007; Devineau et al. 2010), or feline parvovirus (FVP) which is more common in southern populations and in males (Biek et al. 2002). Adult lynx can also be affected by hypothyroidism (Greer et al. 2003).

Although parasite prevalence and abundance may be high, parasites do not seem to negatively influence the physical condition of individual *L. canadensis* (van Zyll de Jong 1966b). *L. canadensis* is frequently infected by helminths particularly in the small intestine but also in the stomach and the lungs (van Zyll de Jong 1966b; Smith et al. 1986). *L. canadensis* can also be host to protozoans, nematodes, cestodes, trematodes, and acanthocephalans (Chitwood 1933; Rausch et al. 1956; van Zyll de Jong 1966b; Schmidt 1968; Forest et al. 2000; Labelle et al. 2001; Simon et al. 2013). The nematode *Trichinella nativa* is widespread in wild *L. canadensis* and its prevalence is correlated with age (Zarnke et al. 1995). *L. canadensis* may be infected by ectoparasites such as fleas and louse (Hopkins 1960; van Zyll de Jong 1966b). The low occurrence of fleas may be related to *L. canadensis* behavior which, instead of using dens regularly, beds on snowshoe hare trails (van Zyll de Jong 1966b).

Interspecific interactions.—Where both species co-occur, exploitation competition may occur between *Lynx rufus* and *L. canadensis* (Buskirk et al. 2000) because the diets of both predators include snowshoe hares. *L. canadensis* populations may decline when *L. rufus* populations increase (de Vos and Matel 1952; Parker et al. 1983; Hoving et al. 2003). Furthermore, exploitation competition may occur between *L. canadensis* and birds of prey or coyote (Buskirk et al. 2000). However, *L. canadensis* is positively associated with the presence of large canids such as wolf (Litvaitis and Harrison 1989) as they may dampen coyote populations (Buskirk et al. 2000). *L. canadensis* can be affected by human activity and roads that provide access to generalist predators (Aubry et al. 2000; Bayne et al. 2008), competition with *L. rufus* or other carnivores (Buskirk et al. 2000; Bayne et al. 2008), and changes in landscape features facilitating generalist predators (Aubry et al. 2000; Buskirk et al. 2000).

Miscellaneous.—Presence of *Lynx canadensis* can be detected via DNA analysis of hairs (Mills et al. 2000; Pilgrim et al. 2005; McKelvey et al. 2006) or during winter via snow-tracking (Koehler 1990; Koehler and Brittell 1990). *L. canadensis* is considered easy to capture, and can be harvested with kill-type traps, snares, or restraining traps (Saunders 1963a; Nellis et al. 1972; Mowat et al. 1994; Proulx et al. 1995). *L. canadensis* is attracted by flesh bait such as meat of snowshoe hares, beaver (*Castor canadensis*), or game birds, and lured with scents such as catnip oil (McDaniel et al. 2000). *L. canadensis* may be captured incidentally in traps set for red fox, coyote, American marten, or fisher (de Vos and Matel 1952; Quinn and Thompson 1987).

Lynx canadensis has long been prized for its soft and valuable fur, and wherever it is common, *L. canadensis* is harvested for its pelt (Quinn and Thompson 1987; Poole 1994). It has been harvested for fur since 1700 and before the 20th century, a distinction between *L. canadensis* and *L. rufus* was not always made. The highest number of *L. canadensis* harvested was reached in 1867 with a total of 95,801 individuals. The average pelt price in Canada has fluctuated greatly, decreasing from $121.29 in 1943–1944 to $5.39 in 1953–1954 before increasing from $28 in 1970–1971 to $191 in 1978–1979 (Novak et al. 1987). The meat of *L. canadensis* is succulent and highly prized locally (Denis 1964).

Age and sex structure of the harvest can be changed by modifying the period of the open harvest season (Quinn and Thompson 1985). Two strategies have been suggested to manage *L. canadensis*: first, its tracking strategy suggests limiting or eliminating trapping for a period of 3–4 years during periods of low snowshoe hare density (second year after the peak in harvest—Parker et al. 1983; Ward and Krebs 1985; Poole 1994) to allow greater harvest during peak (Brand and Keith 1979). The second strategy consists of maintaining untrapped refugium all year long or at least during periods of low snowshoe hare density (Ward and Krebs 1985; Bailey et al. 1986) without suspension of trapping (Poole 1994). *L. canadensis* harvest may also be regulated by quotas (Quinn and Thompson 1987). Managers should monitor *L. canadensis* recruitment instead of snowshoe hare trends to make decisions (Mowat et al. 1996b) which can be done using the total length of the pelt measured from tip of nose to base of tail (Quinn and Gardner 1984).

Lynx canadensis may be aged by tooth replacement and cranial characteristics (Saunders 1964), tooth cementum layers (Nellis et al. 1972; Chubbs and Phillips 1993), or ossification of epiphyseal plates of long bones (Saunders 1964). Kittens may be differentiated from yearlings and adults by the presence of an apical root foramen in canines (Saunders 1964) or by the total length of the pelt, measured from tip of nose to base of tail (< 81 cm—Quinn and Gardner 1984).

HUSBANDRY

Recommended minimum enclosure size per *Lynx canadensis* is 4 by 2 by 2.5 m (l by w by h) and floor area should be increased by 50% for each additional cat (Mellen 1997). Individuals should have access to at least 75% of the vertical space (Mellen 1997) along with several hiding locations (Fanson and Wielebnowski 2013). Clawing activity should be stimulated by providing rotting logs in the enclosure (Mellen 1997). Feeding *L. canadensis* 2 days per week with bones with meat attached, helps stimulate teeth and gums; fasting days are not recommended (Mellen 1997).

In captivity, *L. canadensis* seems less likely to reproduce when maintained in groups larger than as a pair (Mellen 1991). However, interactions between the cats and their keepers increased successful reproduction (Mellen 1991).

Captive born kittens should never be intentionally hand-reared but if done, they should remain with their mother until at least 8–10 days of age (Edwards and Hawes 1997; P. Andrews, in litt.). Kittens can be feed with commercial milk replacers and electrolytes can be given to weak neonates (P. Andrews, in litt.). Solid food can be gradually introduced at 7–8 weeks (P. Andrews, in litt.).

For research, *L. canadensis* can be chemically immobilized using ketamine (Ward and Krebs 1985; Koehler 1990), phencyclidine hydrochloride (Berrie 1972), a mixture of ketamine and xylazine (Squires et al. 2004; Burdett et al. 2007), ketamine and medetomidine (Rockhill et al. 2011), tiletamine hydrochloride and zolazepam hydrochloride (Poole et al. 1993, 1998), ketamine hydrochloride and midazolam hydrochloride (Forest et al. 2000), or phencyclidine hydrochloride and promazine hydrochloride (Carbyn and Patriquin 1983). *L. canadensis* can be euthanized with yohimbine (Greer et al. 2003) or pentobarbital (Poole et al. 1998). Vaccination with porcine zone pellucida does not work for contraception in captive *L. canadensis* (Harrenstien et al. 2004).

BEHAVIOR

Grouping behavior.—*Lynx canadensis* is generally solitary except mother-kit groups (Carbyn and Patriquin 1983; Parker et al. 1983; Mowat and Slough 1998). Hunting groups are more efficient in killing snowshoe hares (O'Donoghue et al. 1998a) and success increases with group size (Parker et al. 1983). Adult groups of 2–5 individuals occur especially, during low snowshoe hare densities (Barash 1971; Mowat and Slough 1998; O'Donoghue et al. 1998a). *L. canadensis* groups usually travel single file in areas where prey are scarce and spread apart when entering habitat with an abundance of prey (Saunders 1963b; Parker et al. 1983). During hunting, individuals fan out up to 10 m apart and reunite after a kill (Mowat and Slough 1998).

Reproductive behavior.—*Lynx canadensis* kittens stay with their mother generally until the next breeding season (Carbyn and Patriquin 1983). Kittens spend a lot of time playing (Saunders 1963a) and related females maintain a bond (Breitenmoser et al. 1993; Slough and Mowat 1996; Mowat and Slough 1998). Litter mates may stay together after leaving their mother (Mowat and Slough 1998) but female offspring tend to remain within their mother's home range while young males disperse away from their mother's area (Breitenmoser et al. 1993; Slough and Mowat 1996). Female kittens can

even stay with their mother if the mother has given birth again (Mowat and Slough 1998). After a snowshoe hare crash, male and female offspring are tolerated in the mother's home range (Breitenmoser et al. 1993; Slough and Mowat 1996). Kittens have been observed to disperse in March (Quinn and Thompson 1985; Poole 1995), April (Mowat et al. 1996b), May, October, and November (Poole 1997). Kittens generally disperse 2–5 weeks before their first birthday (Poole 1995) and the earliest kitten dispersal was at 10 months of age (Parker et al. 1983; Mowat et al. 1996b; Slough and Mowat 1996) while the latest was at 17 months old (Poole 1997).

Communication.—Adult *Lynx canadensis* mark their home ranges using feces, sprayed urine, or anal secretions (Saunders 1963a). Urine scent marks are made every 45–91 m (Saunders 1963a). Kittens bury scat, contrary to adults (Saunders 1963a). *L. canadensis* also communicate by using three different vocalizations: long wailing calls during the mating period (March–April), warning growls when captured, or 5–10 short barks when in family groups (Mowat and Slough 1998).

Miscellaneous behavior.—Hunting behavior of *Lynx canadensis* varies according to snowshoe hare densities. During snowshoe hare abundance, *L. canadensis* uses more snowshoe hare trails and kills more than required (O'Donoghue et al. 1998a, 1998b). *L. canadensis* may cache snowshoe hares during years of great abundance (Nellis and Keith 1968) and return to caches within 2 days (O'Donoghue et al. 1998b). During snowshoe hare decline, *L. canadensis* does not increase its active time (O'Donoghue et al. 1998b) but may increase its foraging time and concentrate its foraging effort in areas of high snowshoe hare densities (Ward and Krebs 1985). During a decline, *L. canadensis* uses four times more hunting beds (O'Donoghue et al. 1998a) and chases are longer (O'Donoghue et al. 1998b). During declines in snowshoe hare density, *L. canadensis* also expands its home range (Ward and Krebs 1985) and becomes more territorial (Stenseth et al. 1997). However, below a certain density of snowshoe hares, *L. canadensis* becomes nomadic and concentrates in abundant snowshoe hare pockets (Bergerud 1971; Brand et al. 1976; Ward and Krebs 1985) or where carrion is abundant (Saunders 1963b). They also become more tolerant of others (Brand et al. 1976). Most adult *L. canadensis* disperse in the first two winters after snowshoe hare population decline (Poole 1997). During that time, its physical condition deteriorates (Parker et al. 1983), leading to reduction and complete cessation in reproduction (Nellis et al. 1972; Brand et al. 1976). At the end of the second winter of declining snowshoe hare number, most of the remaining *L. canadensis* have died (Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). During periods of declining *L. canadensis* densities, trapping vulnerability (Ward and Krebs 1985) and starvation increase (Brand et al. 1976; Parker et al. 1983) while cannibalism may appear (Mowat and Slough 1998).

Morphology and hunting behavior of *L. canadensis* is specialized for snowshoe hares (Brand et al. 1976) and it is an efficient predator because of the lower foot-load of hares (Murray and Boutin 1991). It hunts primarily by sight but also by sound

(Saunders 1963a, 1963b). *L. canadensis* hunts snowshoe hares by stalking, ambushing (Murray et al. 1995; O'Donoghue et al. 1998a; Squires and Ruggiero 2007), following snowshoe hare runways, concentrating movements or using waiting beds (Brand et al. 1976). *L. canadensis* uses the ambushing method more when the canopy is dense and the stalking method in sparse cover (Murray et al. 1995). When *L. canadensis* enters snowshoe hare habitat it travels in a more sinuous pattern (Maletzke et al. 2008).

After stalking as close as possible to its prey, *L. canadensis* usually covers the remaining distance with powerful bounds. The number of jumps depends on the species of prey pursued, the capture success, or the prey density (Nellis and Keith 1968; Squires and Ruggiero 2007). It can make up to 14 jumps to capture its prey (O'Donoghue et al. 1995). The distance between two jumps varies between 1.0 m (Murray et al. 1995) and 2.4 m (Squires and Ruggiero 2007).

Lynx canadensis hunting success varies according to many factors. When hunting snowshoe hares, *L. canadensis* has better success when ambushing than stalking (Murray et al. 1995). The distance from the snowshoe hare at the beginning of the chase is an important factor for successful kills (Nellis and Keith 1968). Length of the chase also influences hunting success. Unsuccessful chases are longer than successful ones (O'Donoghue et al. 1998b). *L. canadensis* chases snowshoe hares 0.46–137 m but successful chases seldom exceed 15–33 m (Saunders 1963b; O'Donoghue et al. 1998b; Squires and Ruggiero 2007). Consistency of the snow and sinking depth are also related to the success of the hunt (Nellis and Keith 1968; Murray and Boutin 1991; Stenseth et al. 2004b). Successful kills are influenced by the *L. canadensis* age and its knowledge of the area (Nellis and Keith 1968) or with the season, increasing during winter (Parker et al. 1983). Success also varies according to the snowshoe hare cycle, with success being lower during periods of increasing snowshoe hare densities as surviving *L. canadensis* become skilled at hunting alternative prey species during the low phase and there is a lag before it switches back to its main prey (O'Donoghue et al. 1998b). However, hunting success is more dependent on hunting conditions than snowshoe hare abundance (Parker et al. 1983) and is similar among habitats and vegetative cover (Murray et al. 1994, 1995).

Lynx canadensis hunting success varied from 8% to 36% in Alberta (Nellis and Keith 1968; Brand et al. 1976), 42% in Newfoundland (Saunders 1963b), and from 20.0% to 38.8% in Yukon (Murray et al. 1994; Murray et al. 1995; O'Donoghue et al. 1998b). During increasing and peaking snowshoe hare densities, *L. canadensis* is more successful from hunting beds (46%) than not from beds (27%—Murray et al. 1995). *L. canadensis* kills on average every 15 km traveled per night (Saunders 1963b) ranging from 13 to 32 km (Nellis and Keith 1968).

Lynx canadensis hunts larger animals in various ways. It approaches bedded white-tailed deer and then rushes to subdue and kill (Fuller 2004). Wounded deer may be followed until later captured and killed (Fuller 2004). *L. canadensis* ambushes caribou and then bites on the head, neck, or shoulders (Stephenson et al. 1991). It attacks mule deer by stalking and biting the neck

10–15 cm behind the ears (Poszig et al. 2004). *L. canadensis* first feeds on big game by starting on the neck, then moving to the shoulders and rib cage, and finally consuming the haunches and internal organs (Poszig et al. 2004). It may drag ungulate carcasses before eating (Poszig et al. 2004). Extent of consumption of prey was related to the time between kills rather than prey abundance (Parker et al. 1983).

Lynx canadensis uses ambush beds that consist of loosely packed and ice-encrusted snow (Murray et al. 1995). Beds may be separated by only 23 m (Saunders 1963a) and are at a density between 5.1 and 18.4 beds along a 10-km trail (O'Donoghue et al. 1998b). Ambush beds of *L. canadensis* are usually closer than 10 m from the starting point of the chase (Murray et al. 1995). *L. canadensis* also makes resting beds near recent snowshoe hare activity (Saunders 1963b).

Lynx canadensis can use snowshoe hare runways to travel (Keith and Meslow 1966). They usually use harder and shallower snow to walk (Murray and Boutin 1991) but may be negatively impacted by snowmobile tracks as they give a competitive advantage to the coyote (Bunnell et al. 2006). Although *L. canadensis* can be active through the day, it travels mostly during the night from 2 h before dark to 1 h after dawn (Saunders 1963a). However, in Montana, activity patterns were different between seasons. During winter all *L. canadensis* were more active during the afternoon and early evening when temperatures were highest (Kolbe and Squires 2007). During summer, males and females without kittens were active around the crepuscule and avoided high temperatures, while females with kittens remained active throughout the day (Kolbe and Squires 2007). *L. canadensis* is active 41.5% of the time (O'Donoghue et al. 1998b) and is mostly in search of food during its active hours (Brand et al. 1976). A kill is usually followed by a period of inactivity (Parker et al. 1983) and hunting is resumed following consumption of its last kill (Saunders 1963b). It is more active at its kill around midnight and late in the morning (Poszig et al. 2004). *L. canadensis* decreases activity during a storm (Saunders 1963a).

Lynx canadensis is a good swimmer (Denis 1964). When swimming, it may be low in the water or have its back raised and can cover up to 3.2 km (Denis 1964).

GENETICS

The karyotype of *Lynx canadensis* is indistinguishable from that of the domestic cat. It has a diploid number (2n) of 38 chromosomes, a fundamental number of 72, with 16 pairs of metacentrics, 16 pairs of submetacentrics, and 4 acrocentrics (Benirschke et al. 1966). The Y and X chromosomes are, respectively, a small meta- or submetacentric and medium-sized submetacentric (Wurster and Benirschke 1968; Hsu and Benirschke 1974). G-banded karyotypes can be used to differentiate *L. canadensis* from the domestic cat but G-bands are identical among *Lynx* species (Wurster-Hill and Certerwall 1982).

Microsatellite loci may be useful in population genetic studies of *L. canadensis* (Carmichael et al. 2000). In a comparison

between core populations and peripheral populations using nine microsatellite loci, peripheral populations exhibited decreased genetic variation in the form of fewer mean numbers of alleles and lower expected heterozygosity (Schwartz et al. 2003). The genetic structuring of *L. Canadensis* is similar over large distances (Schwartz et al. 2002; Row et al. 2012); however, the Rocky Mountains and the Coastal Mountains represent east-west and north-south barriers to gene flow in *L. canadensis* (Rueness et al. 2003). The existence of a geographically invisible barrier in eastern Canada also influences its genetic structure (Rueness et al. 2003). Thus *L. canadensis* genetically seems to be divided into the same three regions (Atlantic, Continental, and Pacific) that synchronize its cycle in density. Restriction fragment patterns of the 16S rRNA can be used to differentiate *L. canadensis* from all other North America felid species (Mills et al. 2000).

The mitochondrial genome and the nuclear genome have been sequenced. The mitochondrial genome (NCBI, BioProject, Accession Number NC_028313) and nuclear genome (NCBI, BioProject, Accession Number PRJNA533815) are entered in GenBank.

Wild female *L. canadensis* can mate with wild *L. rufus* males (Schwartz et al. 2004; Homyack et al. 2008). Hybrids of *L. canadensis*–*L. rufus* may reproduce successfully (Homyack et al. 2008). Hybrids have intermediate physical characteristic like intermediate paw size, intermediate tail color, or intermediate hind foot length, and mixed physical characteristics like a *L. rufus* pelage and *L. canadensis* ear tufts length (Homyack et al. 2008).

CONSERVATION

Lynx canadensis is listed as "Least Concern" by the International Union for the Conservation of Nature and Natural Resources, is on Appendix II of the Convention on International Trade in Endangered Species, and its population trend is considered stable (United Nations Environment Programme-World Conservation Monitoring Center 2009; Vashon 2016). However, it is listed as "Endangered" in New Brunswick and Nova Scotia under the New Brunswick Species at Risk Act and Nova Scotia's Endangered Species Act. In the United States, *L. canadensis* was listed in 2000 as "Threatened" under the Endangered Species Act (Vashon et al. 2008a).

Lynx canadensis has successfully been reintroduced to Colorado (Devineau et al. 2010) even though the first attempt most likely failed because of high mortalities due to starvation (Shenk 2001). In the Adirondack Mountains of New York, the failure of its reintroduction appears to be related to high road mortality (Hoving et al. 2005). When planning a reintroduction program for *L. canadensis*, five factors should be examined to increase the success: (1) a release protocol focused on reducing dispersal rates from the reintroduced population, (2) mortality induced by anthropogenic factors, (3) phase of the snowshoe hare cycle when reintroduction occurs, (4) duration of the release program, and (5) number of animals released (Steury and Murray 2004). *L. canadensis* should be released during the decline phase of the snowshoe hare

cycle (Steury and Murray 2004) as each individual requires at least 1.1–1.8 snowshoe hares/ha to persist (Steury and Murray 2004). This allows the *L. canadensis* population to increase along with the hare population. The success of the reintroduction may be increased by placing individuals in holding facilities for a minimum of 3 weeks, or until physical condition is optimal and the animals have acclimated to the new area (Shenk 2001). Reintroduction should be performed in central areas of *L. canadensis* habitat range before trying at the periphery (Scott et al. 1999).

The conservation and recovery of *L. canadensis* populations in the southern portion of its range require the protection of large snowshoe hare habitat and ensuring connectivity between *L. canadensis* populations (Murray et al. 2008; Squires et al. 2013). Forests should be managed to give a temporal and spatial mosaic of forest age classes, which can be done with fires, logging, and timber thinning (Koehler and Brittell 1990). Thus, fire management has the potential to have an impact on *L. canadensis* abundance (Paragi et al. 1997).

Climate change, through climate warming and snowfall decrease, may give *L. canadensis* less competitive advantage over bobcats and decreases prey vulnerability (Hoving et al. 2003). In the future, this could result in stronger declines for populations at the southern edge of their distribution due to climate change than projected logging or exploitation rates (Carroll 2007). During the last century, *L. canadensis* distribution has contracted (McKelvey et al. 2000a), this might be due to the reduction of large forest fires, with human-caused fire suppression, resulting in limitation of early successional forest, which are an important habitat for snowshoe hares (Koehler 1990). Other hypotheses are: climate change (Koen et al. 2014), competition with terrestrial predators, roads and human mortality, reduced habitat quality, increased habitat fragmentation, and reduced in connectivity with northern population (Aubry et al. 2000; Buskirk et al. 2000; McKelvey et al. 2000b; Mowat et al. 2000).

ACKNOWLEDGMENTS

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