

Climbing behavior of northern red-backed voles (*Myodes rutilus*) and scansoriality in *Myodes* (Rodentia, Cricetidae)

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Scansoriality (climbing) allows access to valuable resources in the arboreal niche and is widespread among mammals, yet little is known about how it originates from obligate terrestriality. The northern red-backed vole (*Myodes rutilus*) is a small, Holarctic rodent long presumed to be strictly terrestrial, yet 3 of its congeners (*M. gapperi*, *M. glareolus*, and *M. californicus*) have been observed climbing in trees. We conducted paired arboreal and ground trapping surveys in interior Alaska to investigate anecdotal accounts of tree-climbing behavior in *M. rutilus*. Results indicate that they readily climb up to 2 m above ground in trees of their own volition, a phenomenon heretofore undocumented in the literature. Camera trap videos show *M. rutilus* exhibiting behavior and dexterity—such as terminal branch arboreal quadrupedalism and head-first descent mediated by hindfoot rotation—generally associated with more arboreal species. Northern red-backed voles may therefore provide a new perspective on early stages of scansoriality in small-bodied mammals.

Key words: Alaska, arboreal, Arvicolinae, climbing, Myodes rutilus, northern red-backed vole, scansorial

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Scansoriality, the ability or propensity to climb, is believed to have evolved independently in multiple extant and extinct mammal lineages (Jenkins and McClearn 1984), yet little is known about the intermediate stages between obligate terrestriality and arboreality (tree-dwelling). Recent paleontological research has demonstrated a long history of climbing in mammals (Luo 2007), and some authors have concluded that scansoriality is plesiomorphic in placental mammals (O'Leary et al. 2013). However, the behavioral and ecological transitions from obligate terrestriality to scansoriality remain poorly studied outside of putative models specific to primate origins (Gebo 2004; Sargis et al. 2007). Studies of scansoriality in small mammals, particularly in species demonstrating incipient climbing ability after recent divergence from a terrestrial common ancestor, provide a window into this important evolutionary transition.

Characters commonly associated with climbing include elongated phalanges, deeper claw curvature, a more gracile appendicular skeleton, increased joint mobility, elongated and often prehensile tails, and in some cases an opposable hallux (Cartmill 1985; Sargis 2002a, 2002b; Kirk et al. 2008). These are thought to be better developed in larger-bodied mammals (Jenkins 1974), and indeed results from morphological studies have found minimal differentiation in some of these characters between small (i.e., < 75 g) terrestrial and arboreal species, particularly in rodents (Kirk et al. 2008; Samuels and Van Valkenburgh 2008). Regardless, there are many scansorial small-bodied (< 75 g) placental species. Some represent the most diminutive of their order, such as the least weasel (Mustela nivalis, Carnivora-Sheffield and King 1994) and mouse lemurs (Microcebus spp., Primates-Radespiel et al. 2006), or functional outliers like the alpine shrew (Sorex alpinus, Soricomorpha-Hutterer 1985). Many small rodents are also skilled climbers, including the familiar North American deer mouse Peromyscus maniculatus (Horner 1954) and the golden mouse Ochrotomys nuttalli (Linzey and Packard 1977). Two species of tree voles-the red tree vole (Arborimus longicaudus) and the sonoma tree vole (A. pomo; Rodentia, Cricetidae)—are fully arboreal, living in large conifers and rarely descending to the ground (Hayes 1996; Swingle et al. 2005). The 3rd Arborimus species, the white-footed vole (A. albipes) is also known to nest in trees up to 13 m above ground (Forsman and Swingle 2006).

Voles and lemmings (Cricetidae, Arvicolinae) occupy a variety of ecological niches despite a superficially conserved body plan (Hall 1981). Although primarily terrestrial or semifossorial, some species are semiaquatic (*Arvicola* spp., *Microtus richardsoni*) or arboreal (*A. longicaudus*). Red-backed voles (*Myodes* spp.) include 12 species (Musser and Carlton 2005) whose ranges form a mosaic across the Northern Hemisphere.



These small-bodied (< 50 g) rodents have relatively short legs and tails less than one-half their body length (Merritt 1981; Alexander and Verts 1992)—features not commonly associated with climbing. Although *Myodes* is generally considered to be terrestrial, 3 species—the bank vole (*M. glareolus*), the southern red-backed vole (*M. gapperi*), and the western red-backed vole (*M. californicus*)—are known to occasionally climb trees (Getz and Ginsberg 1968; Holisova 1969; Swingle 2005).

Climbing in the European species *M. glareolus* has been observed in England (Montgomery 1980; Tattersall and Whitbread 1994; Buesching et al. 2008) and the Czech Republic (Holisova 1969). In all of these studies, *M. glareolus* was found to regularly climb trees, although consistently less often than other sympatric and more scansorial species such as the yellow-necked field mouse, *Apodemus flavicollis* (Muridae, Murinae). Nevertheless, *M. glareolus* was captured up to 5 m above the ground on the Isle of Wight (Tattersall and Whitbread 1994), suggesting considerable climbing ability.

M. gapperi was first reported climbing in a large sub-alpine fir (Abies lasiocarpa) on Mount Rainier, Washington, where an individual was observed frequenting a nest 4.6 m above ground (Shaw 1924). An individual near Prince George, British Columbia, was observed sunning on a branch 6.1 m above the ground "in much the same pose assumed by basking marmots" before retreating to a nest in the same tree (Grant 1957:88). Several southern red-backed voles were captured in trees in traps set for flying squirrels (Glaucomys spp.) during the winter of 1959–1960 near North Amherst, Massachusetts (Muul and Carlson 1963). Getz and Ginsberg (1968) conducted a field- and captive-based study to examine the use of 3-dimensional habitat by *M. gapperi*. In the field, southern red-backed voles were captured in traps up to 1.5 m above ground, while in the lab, they were recorded climbing on artificial branches and using above-ground nest boxes (Getz and Ginsberg 1968). As in M. glareolus, M. gapperi was also found to climb less frequently than sympatric species presumably better adapted to climbing, namely the white-footed mouse, Peromyscus leucopus (Cricetidae, Neotominae).

Only 1 brief yet significant report of climbing in the western red-backed vole (*M. californicus*) has been published. Between June 2002 and September 2003, while monitoring the activity of red tree vole (*A. longicaudus*) nests in western Oregon, Swingle (2005) discovered a single *M. californicus* inhabiting a nest 10.8 m above the ground in a Douglas-fir (*Pseudotsuga menziesii*). This nest contained sign of recent activity by *A. lon-gicaudus*, including fresh clippings of Douglas-fir needles, the preferred food of this arboreal vole. At over 10 m, this is the highest reported sighting of any *Myodes* species and suggests that *M. californicus* is a proficient climber, though the lack of other sightings during Swingle's (2005) study suggests that occupation of red tree vole nests by *M. californicus* is uncommon.

The northern red-backed vole (*Myodes rutilus*) has a Holarctic distribution and is abundant across Alaska's boreal forest and other habitats. Only 2 accounts of climbing in this species have been published: an anecdotal account in a

self-published natural history book (Smith 2008) and a newspaper article in which the author describes observing a northern red-backed vole climbing in a black spruce (Picea mariana) on a cold (-40°C) day in Fairbanks, Alaska (Rozell 2006). Similar to Getz and Ginsberg (1968), one of us (LEO) was surprised to capture several northern red-backed voles in arboreal traps set for northern flying squirrels (Glaucomys sabrinus) near Fairbanks, Alaska, in 2011. Fur trappers and bird enthusiasts in interior Alaska have reported observations of M. rutilus in trees to us. These reports, along with published accounts of climbing in 3 congeners, suggest northern red-backed voles, and possibly the entire genus Myodes, may be more scansorial than previously thought. Additionally, throughout most of its range in Alaska, M. rutilus faces no competition from any similarly sized scansorial or arboreal mammal. We investigated the climbing behavior of *M. rutilus* in interior Alaska, testing our prediction that the species uses the arboreal niche to add a 3rd dimension to its habitat.

MATERIALS AND METHODS

Trapping.—Trapping was conducted on 3 separate occasions at 2 locations in interior Alaska during the summer and fall of 2012. All captured animals were collected and deposited as voucher specimens in the University of Alaska Museum (UAM) Mammal Collection and are reported in Appendix I. All activities were conducted under UAM's scientific collecting permit (#12–078) issued by the Alaska Department of Fish and Game's Division of Wildlife Conservation and in accordance with the American Society of Mammalogists' Animal Care and Use Guidelines (Sikes et al. 2011) and the University of Alaska Fairbanks IACUC (assurance #152295-12). All traps were baited with rolled oats and peanut butter and were checked every 12h.

On 5 July 2012, 40 Sherman traps $(3 \times 3.5 \times 9'';$ H.B. Sherman Traps Inc., Tallahassee, Florida) were placed on branches in a black spruce forest 30 km northwest of Fairbanks, Alaska ("Cache Creek"; Table 1). Traps were placed horizontally on branches 1–5 m above the ground, with the doors facing the trunk. The diameter at breast height (DBH) of the trees ranged from 10 to 30 cm, and the diameter of the branches where traps were placed ranged from 2 to 5 cm. Only 1 trap was placed in each tree. Traps were spaced approximately 10 m apart, depending on horizontal branch availability. Traps were secured to the branches using a strip of Velcro (Velcro Industries, Manchester, New Hampshire) one-wrap and were opened from 5–8 July for a total of 120 trap nights.

On 9 August 2012, 50 Sherman traps were set in a sub-alpine white spruce (*Picea glauca*) stand near Twelvemile Summit, 100 km northeast of Fairbanks, Alaska ("Twelvemile Summit"; Table 1) using the methods described above. Trees in this location were generally larger (DBH 10–40 cm) than those at Cache Creek, while branch diameter ranged from 2 to 8 cm. In order to compare the number of *M. rutilus* caught in traps placed in trees to those caught on the ground, an additional 50 traps were set on the ground near the arboreal trap line. Traps were opened from 9–13 August for a total of 400 trap nights.

Survey area	Dates	Location	Trap type	Arboreal trapnights	Terrestrial trapnights	Results (A or T)
Cache Creek	5–8 July 2012	64°51′51′N 148°22′8′W	Sherman	150	Х	2 Myodes rutilus (A)
Twelvemile Summit	9–13 August 2012	65°23′11′N 146°1′43′W	Sherman	200	200	2 Myodes rutilus (A) 10 Myodes rutilus (T) 2 Microtus oeconomus (T)
Twelvemile Summit	21–23 September 2012	65°23′11′N 146°1′43′W	Museum Special	100	100	10 Myodes rutilus (A) 16 Myodes rutilus (T) 1 Microtus xanthognathus (T

 Table 1.—Summary of fieldwork. Voucher specimens collected are described as A (arboreal) or T (terrestrial). X: No terrestrial trapping was conducted at Cache Creek.

On 22 September 2012, trapping at Twelvemile Summit was repeated in the same location using 50 Museum Special snap traps (Woodstream Corporation, Lititz, Pennsylvania) positioned with bait pans facing the trunk of the tree. Paired traplines (1 on the ground, 1 in trees) were set in the same arrangement as the August session. Traps were opened from 21–23 September for a total or 200 trap nights.

Climbing in *Myodes* species has been monitored with snap traps (Getz and Ginsberg 1968) and live traps (Tattersall and Whitbread 1994) but never with both in the same location. We compared trapping success with live and snap traps from our

Twelvemile Summit location using 2-proportion *z*-tests. The formula $z = \frac{P_1 - P_2}{SE}$ was used to determine the *z* scores, which were

then converted to *P* values using a normal distribution table.

Video.-Although far more commonly used to monitor and observe large-bodied species, video monitoring has been shown to be useful for studying smaller-bodied taxa as well (Malt and Lank 2007), including voles (A. longicaudus-Forsman et al. 2009). On 27 November-1 December 2012 and 31 March-3 April 2013, 3 Bushnell HD Trophy Max camera traps (Bushnell Corporation, Overland Park, Missouri) were set 1-2 m from black spruce (P. mariana) and quaking aspen (Populus tremuloides) tree trunks in areas with signs of high vole activity (snow tunnel entrances, tracks, etc.) in and around Fairbanks, Alaska. Small (approximately 10g) portions of peanut butter were placed at 10-cm intervals from 10-70 cm high directly on the trunks as bait and camera traps were installed 1–2 m away set to the highest trigger sensitivity. Video recordings with location data were deposited in the UAM Mammal Observation Collection and are accessible on the online database Arctos (http://arctos.database.museum/home.cfm). See Appendix II for catalog numbers and location coordinates.

RESULTS

Trapping.—In the 1st trapping session (5–8 July 2012), 2 northern red-backed voles were captured on consecutive nights. Both captures occurred in the same trap 2.3 m above ground in a white spruce (DBH 10 cm). These were the only arboreal captures at this location.

During the 2nd trapping session (9–13 August 2012), 2 northern red-backed voles were captured in different arboreal traps, both over 1.8 m off the ground in white spruce (DBH

Table 2.—Results from a 2-proportion *z*-test for difference between success of Sherman live traps and Museum Special snap traps in arboreal and terrestrial placement at Twelvemile Summit. All results are significant at $\alpha = 0.05$. See Table 1 for coordinates, dates, and species captured. Cache Creek results are not included in this analysis.

Trapping method	Sherman traps: captures/ trapnights (p ₁)	Museum special traps: captures/ trapnights (p ₂)	z score	P value
Arboreal	2/200 (0.01)	10/100 (0.10)	-6.423	0.0001
Terrestrial	12/200 (0.06)	16/100 (0.16)	-2.087	0.005
Total	14/400	27/200	-4.576	0.0001

30–38 cm). Ground traps captured 10 *M. rutilus* as well as 2 root voles (*Microtus oeconomus*). No root voles were captured in the arboreal traps.

Trap success increased in the 3rd trapping session (21–23 September 2012), with 10 *M. rutilus* captured in arboreal traps and 16 in ground traps. All arboreal captures were in white spruce (DBH 14–65 cm), and trap height ranged from 1.5 to 1.8 m above ground. One taiga vole (*Microtus xanthognathus*; UAM Mammal Collection Number UAM 115676) was also captured on the ground. No other species were captured during this session.

Trapping success was higher with Museum Special traps than with Sherman traps at the Twelvemile Summit location (Table 2), with significantly more captures in both terrestrial traps (P = 0.005) and arboreal traps (P < 0.0001).

Video.—Camera trap videos from 27 November-1 December 2012 and 31 March-3 April 2013 show M. rutilus readily climbing directly up the trunks of trees to access bait (Fig. 1). Video also shows northern red-backed voles moving horizontally around the trunk of a quaking aspen (UAM Mammal Observation Number UAMObs:Mamm:185) and ascending a white spruce by leaping up and grasping horizontal branches with its forelimbs and pulling itself up (UAMObs:Mamm:195). One recording shows a M. rutilus climbing up an unbaited black spruce in the background (i.e., not the targeted tree; UAMObs:Mamm:195). Several videos show a vole climbing away from the trunk far out onto small horizontal branches ("terminal branch arboreal quadrupedalism" sensu Byron et al. 2011; UAMObs:Mamm:195). One vole climbs out on an narrow branch in order to consume old man's beard lichen (Usnea lapponica, UAM Herbarium Catalog Number UAMb:Herb:48848; UAMObs:Mamm:195). Additionally, northern red-backed



Fig. 1.—Northern red-backed vole (*Myodes rutilus*) ascending a quaking aspen to access bait, April 2013, Fairbanks, Alaska. Still image taken from UAMObs:Mamm:186.



Fig. 2.—Northern red-backed vole (*Myodes rutilus*) descending a quaking aspen, April 2013, Fairbanks, Alaska. Note head-first orientation and hindfoot rotation used to gain purchase on the relatively smooth bark. Still image taken from UAMObs:Mamm:185.

voles were recorded descending both the black spruce and quaking aspen head first while supporting their weight by laterally rotating their hindfeet, enabling the rear claws to grasp the substrate (Fig. 2). This is the 1st published report of hindfoot rotation in any arvicoline species and only the 2nd report of head-first descent (the other being in *A. longicaudus*—Forsman et al. 2009).

DISCUSSION

Three members of the genus *Myodes* (*M. gapperi*, *M. glareolus*, and *M. californicus*) have been documented climbing trees (Getz and Ginsberg 1968; Holisova 1969; Swingle 2005). We confirm that *M. rutilus* also readily ascends as high as 2 m above ground in trees, making it the 4th *Myodes* species known to climb. We also show that *M. rutilus* climbs trees regardless of the presence of bait. The frequency of arboreal captures as well as the agility shown in camera trap videos suggest that northern red-backed voles in interior Alaska are adept at acquiring resources off the ground.

Museum Special traps were more successful than Sherman live traps in both ground and arboreal trap lines (Table 2). Although this difference in trap success has been observed before (e.g., Eulinger and Burt 2011), it may be due to a seasonal fluctuation in population size. M. rutilus populations are known to increase from May to September (Gilbert and Krebs 1991), and in this study, Sherman traps were used in July and August, while Museum Special traps were used in September. Nevertheless, Museum Special traps proved to be much more efficient than Sherman traps for the arboreal trap lines. Successful placement of the Sherman trap in a tree requires a flat, sturdy branch, a feature that can be difficult to find on relatively small spruce trees (Picea spp.), which are common in interior Alaska. Museum Specials can be attached to downward-sloping and/or uneven branches, which increases trap placement opportunities and allows for more evenly spaced traps. These traps also provided information about the climbing ability of *M. rutilus*, as some voles were captured in traps that required animals to cross narrow branches or descend uneven surfaces (UAM 115691, 115697).

Camera traps recorded numerous instances of M. rutilus climbing up and down tree trunks as well as moving across small branches. Our documentation of head-first descent of tree trunks is particularly notable. Multiple videos captured northern red-backed voles descending head first using their laterally rotated hindfeet to secure themselves to the substrate and, presumably, moderate their speed (Fig. 2; UAMObs:Mamm:185, UAMObs:Mamm:194). The hindfeet are seen to rotate by plantarflexing the foot while simultaneously inverting it (Fig. 2). This movement has been documented in other scansorial rodents such as the eastern grey squirrel (Sciurus carolinensis-Jenkins and McClearn 1984) but has not to our knowledge been described in any arvicoline. Moreover, M. rutilus is capable of head-first descent not only on relatively rough-barked spruce trees but also on quaking aspen, which has relatively smooth bark. We also observed grasping with the hands and feet while climbing across small branches (< 1 cm in diameter) to access lichen (UAMObs:Mamm:195). One M. rutilus was also seen leaping up from a small branch to grasp another before pulling itself up (UAMObs:Mamm:195), a behavior described in lemurs as "bimanual movement" (Gebo 1987:273).

Northern red-backed voles used their tails in 2 different ways while climbing. During ascent, they braced their relatively short tails against the tree for apparent stabilization (UAMObs:Mamm:185) in a manner reminiscent of the North American porcupine, *Erethizon dorsatum* (Roze 2009). While crossing small branches, they appeared to use their tails as a counter-balance by moving it from one side to the other (UAMObs:Mamm:196). Using the tail in this latter manner is considered a climbing adaptation (Cartmill 1985) and has been seen in other scansorial North American cricetids (e.g., *Peromyscus*—Horner 1954). These findings warrant further research into the morphological adaptations to climbing (i.e., joint mobility, tail myology, metapodial proportions, etc.) in *M. rutilus* and other arvicolines.

Climbing allows access to resources above ground. A camera trap video from December 2012 shows a vole climbing up a trunk and out on a small branch to consume lichen (UAMObs:Mamm:195). While only making up a small fraction of the summertime diet, lichen plays an increasingly important role in the diet of *M. rutilus* in Alaska in autumn, rising from 7% of the diet in July to 23% in September (Bangs 1984). Unfortunately, these data do not extend past September, and very little is known about the diet of Alaskan *M. rutilus* in winter, although the increased consumption of lichen in the fall and its year-round presence in trees suggests that *M. rutilus* may rely on lichen as a food source in winter.

Other reasons for climbing include nesting and escaping from competition, predation, or both. Two accounts of climbing in *M. gapperi*, both from the month of July, reported nests made of lichen or moss (Shaw 1924; Grant 1957). Arboreal nests have not been reported for *M. rutilus*. Climbing may be a way to avoid predation. A captive study of least weasel (*M. nivalis*) predation on bank voles (*M. glareolus*) found the latter to regularly climb artificial "trees" to avoid being caught while the sympatric field vole (*Microtus agrestis*) did not (Erlinge 1975). This tactic may also be used by *M. rutilus*, since least weasels are common in Alaska.

Members of the genus Myodes that are known to climb are consistently outperformed by other sympatric scansorial species such as P. leucopus (sympatric with M. gapperi) and A. flavicollis (sympatric with M. glareolus). There are no other scansorial mammals similar in size to M. rutilus in interior Alaska, where the next-largest herbivorous arboreal mammal is the northern flying squirrel (G. sabrinus), which also consumes lichen (Wells-Gosling and Heaney 1984). Results from this study suggest that *M. rutilus* may climb more frequently than its North American congener M. gapperi (Getz and Ginsberg 1968), but additional field work is required to determine if this is the case. M. rutilus is sympatric with the scansorial P. maniculatus across a portion of its North American range in the Yukon Territory and British Columbia, Canada. In a portion of southeast Alaska, M. rutilus is also sympatric with the northwestern deer mouse, Peromyscus keeni, a species that has been recorded nesting between 18 and 33 m off the ground in oldgrowth Douglas-fir trees (Malt and Lank 2007). An arboreal trap-based monitoring project in interior Alaska as well as those regions of overlap with *Peromyscus* spp., in combination with research on diet and space partitioning, would help to illuminate how competition influences the ability and propensity to climb in these species.

The subfamily Arvicolinae (Cricetidae) is a Holarctic assemblage of 151 currently recognized species (Musser and Carlton 2005). This lineage is reported to have diverged from a common ancestor 5–6 million years ago (Chaline and Brunet-Lecomte 1999; Conroy and Cook 1999) and, despite a relatively conserved body plan, has diversified into a variety of ecomorphologies throughout its range. These include semi-aquatic (*Ondatra zibethicus*), fossorial (*Microtus ochrogaster*),

obligate arboreal (A. longicaudus), and subnivean (Dicrostonyx groenlandicus) specialists. The genus Myodes, however, has a brief 2- to 3-million-year history defined by periods of climatedriven isolation and speciation in allopatry followed by range expansion and hybridization (Runck et al. 2009; Kohli et al. 2014), resulting in a complex of closely aligned species that exhibit limited morphological and genetic variation. A recent multilocus phylogeny of the tribe Myotini (Myodes Pallas, 1811; Alticola Blanford, 1881; Eothenomys Miller, 1896; Caryomys Thomas, 1911; and Hyperacrius Miller, 1896) did not recover a monophyletic *Myodes*, and the authors proposed that 6 of the 12 Myodes species (M. rufocanus, M. andersoni, M. smithii, M. imaizumii, M. rex, and M. regulus) be reclassified in the genus Craseomys Miller, 1900 (Kohli et al. 2014). Our study confirms the scansorial behavior of 4 of the 6 species in the genus *Myodes* (sensu Kohli et al. 2014); only in the poorly studied M. shanseius of China and M. centralis of China and Kyrgyzstan has scansoriality not been documented.

The evolution of scansoriality in eutherian mammals has been of long-standing interest to paleontologists and primatologists, as the movement from the ground to the trees is thought to have played a significant role in both primate evolution (Jenkins 1974; Gebo 1996) and the diversification of therians (Luo et al. 2011). Additionally, the 2 oldest-known proposed eutherians in the fossil record, both of which are believed to have weighed less than 25 g, are interpreted as having been scansorial (Ji et al. 2002; Luo et al. 2011). Terrestrial and arboreal mammals larger than 100 g show greater morphological disparity in hand proportions (a commonly used indicator of climbing) than do smaller-bodied species (Kirk et al. 2008), which are more appropriate for studying the transition between terrestriality and arboreality in early mammals than the more traditional taxa. Red-backed voles may therefore represent a new small-mammal climbing model for studying these early transitional stages, providing an integral piece of the puzzle that may further illuminate scansorial adaptation in both extant and extinct mammals.

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Appendix I

Specimens collected for this study, ordered by locality, species, and date of capture. See Table 1 for locality data. All specimens are housed in the mammal collection at the University of Alaska Museum. Specimen data can be found on Arctos at http://arctos.database.museum.

Cache Creek.— Myodes rutilus: UAM 114310, 114311

Twelvemile Summit.—*Microtus oeconomus*: UAM 114348, 114349. *Microtus xanthognathus*: UAM 115676. *Myodes rutilus*: UAM 114338, 114339, 114340, 114341, 114342, 114343, 114344, 114345, 114346, 114347, 114350, 114351, 115677, 115678, 115679, 115680, 115681, 115682, 115683, 115684, 115685, 115686, 115687, 115688, 115689, 115690, 115691, 115692, 115693, 115694, 115695, 115696, 115697, 115698, 115725, 115726, 115727, 115914

Appendix II

Video footage captured with Bushnell Trophy Cameras has been archived in the UAM Mammals Observation Collection. Both locations are in Fairbanks, Alaska, and are ordered by date. Observation data and videos can be found on Arctos at http://arctos.database.museum.

64°49′42″N, 148°8′49″W—UAMObs:Mamm:193, 194, 195, 196

64°54′54″N, 147°43′39″W—UAMObs:Mamm:183, 184, 185, 186