**Sylvilagus obscurus** (Lagomorpha: Leporidae)

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**Abstract:** *Sylvilagus obscurus* Chapman, Cramer, Dippenaar, and Robinson, 1992, commonly called the Appalachian cottontail, is distinguished from other syntopic leporids by its black spot between the ears, black fur along the anterior edge of the ears, and reddish-gray sides overlaid with a black wash. One of 22 species in the genus, *S. obscurus* is found across the Appalachian Mountains region, from Pennsylvania to northern Alabama. An inhabitant of habitats with dense woody understory cover such as early successional forests and mature forests with ericaceous shrubs, this rabbit is considered “Near Threatened,” with major threats that include habitat destruction, climate change, and competition with the eastern cottontail, *Sylvilagus floridanus*.

**Key words:** Allegheny cottontail, Appalachian cottontail, leporid, mountain cottontail, wood rabbit

Synonymy completed 1 July 2008
DOI: 10.1093/mspecies/sez018
Version of Record, first published online December 9, 2019, with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.

**Nomenclatural statement.**—A life science identifier (LSID) number was obtained for this publication: urn:lsid:zoobank.org:pub:76A8A425-2E9F-413F-A6A1-7730CAA252B8

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*Sylvilagus obscurus* Chapman, Cramer, Dippenaar, and Robinson, 1992

Appalachian Cottontail


*Sylvilagus (Sylvilagus) floridanus transitionalis*: Lyon, 1903:336. Name combination. Part.


**CONTEXT AND CONTENT.** Order Lagomorpha, family Leporidae, genus *Sylvilagus*, subgenus *Sylvilagus*. There are 22 recognized species within the genus *Sylvilagus* (American Society of Mammalogists 2018). No subspecies are recognized for *S. obscurus* (Hoffmann and Smith 2005).

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common names include Allegheny cottontail, mountain cottontail, and wood rabbit (Whitaker and Hamilton 1998). *Sylvilagus* (i.e., wood rabbit) is derived from the Latin *sylva*, meaning woods and the Greek λαγῶς (*lagōs*), meaning hare (Palmer 1904). *Obscurus*, from the Latin, meaning dusky or secretive, was selected as the species name because of its secretive behavior and similar appearance to *S. transitionalis* (Chapman et al. 1992).

**DIAGNOSIS**

*Sylvilagus obscurus* cannot be distinguished from the New England cottontail *S. transitionalis* based on pelage or external morphology but is separated geographically. *S. obscurus* occurs from Pennsylvania to northern Alabama, whereas *S. transitionalis* is found in New England and southern New York east of the Hudson River (Chapman et al. 1992). *S. obscurus* (2n = 46) differs from *S. transitionalis* (2n = 52) based on chromosome number (Ruedas et al. 1989; Chapman et al. 1992) and subtle cranial and toothrow measurements identified by a discriminant function analysis (Chapman et al. 1992). Mitochondrial DNA markers for *S. obscurus* and *S. transitionalis* are indistinguishable from each other, suggesting recent speciation occurred 11,750 years ago (Litvaitis et al. 1997; Ruedas et al. 2017).

*Sylvilagus obscurus* is sympatric with the eastern cottontail *S. floridanus* across its range (Whitaker and Hamilton 1998). The two species superficially resemble each other, but typically differ in habitat, pelage, size, and skull morphology. *S. floridanus* is found in open habitats with grassy or brushy cover, whereas *S. obscurus* is typically associated with dense shrubby cover in forested areas and mountain balds (Chapman 2007). *S. obscurus* (Fig. 1) has a black spot between the ears and black fur along the anterior edge of the ears in > 90% of individuals, features that are found in < 40% of *S. floridanus* individuals. *S. floridanus* can have a white spot on the forehead, which is not characteristic of adult *S. obscurus* (Litvaitis et al. 1991). *S. obscurus* also has a black wash across the back, creating a penciled-in look that is not present in *S. floridanus*. *S. obscurus* tends to be smaller in size (see “General Characters”) than *S. floridanus* (total length: 395–477 mm; weight: 801–1,533 g—Chapman et al. 1980). The suture between the nasals and frontals on the skull is a smooth line in *S. floridanus* (Chapman et al. 1980) and a jagged and irregular line in *S. obscurus* (Fig. 2).

**GENERAL CHARACTERS**

The head of *Sylvilagus obscurus* typically has a black spot between the ears (Fig. 1). The cheeks have gray-grizzled fur. The ears are rounded with distinct black fur along the anterior edges. The upper sides are reddish-gray during the winter and reddish-brown during the summer overlaid with a black wash, creating a penciled-in rather than a grizzled effect. The venter is light gray to white and the forelegs are rusty rufous (Litvaitis et al. 1991; Chapman et al. 1992; Linzey 2001). Females average 3% longer than males; average total lengths (mm; parenthetical SD and n) were: 412.1 (17.7, 39) for females versus 400.9 (19.5, 24) for males (Davis and Roth 2008). Average external body measurements (mm or g; parenthetical SD, range, and n) for adult males and females, respectively, were: tail length, 42.6 (11.5, 22–57, 7), 47.3 (11.2, 30–65, 7); hind foot length, 93.0 (3.0, 89–97, 7), 92.8 (2.8, 87–96, 9); ear length, 56.7 (2.1, 54–59, 7), 58.2 (3.2, 54–63, 9); and body mass, 887.7 (78.3, 756–965, 7), 924.4 (75.7, 802–1,038, 8—Chapman and Morgan 1973).

The postorbital process narrows to a point that frequently touches the skull (Fig. 2). The frontonasal sutures are jagged and irregular. The skull lacks an anterior supraorbital process and anterior supraorbital notch (Linzev 2001; Chapman 2007). Mean cranial measurements (mm; parenthetical SD and n) for adults were: greatest length of skull, 70.8 (2.1, 91); zygomatic breadth, 36.3 (1.2, 13); postorbital constriction, 14.3 (0.8, 14); length of nasals, 26.6 (2.5, 12); greatest width across nasals, 14.3 (0.8,
Sylvilagus obscurus

14); maxillary toothrow, 13.6 (0.4, 14); breadth of brain case, 22.9 (0.6, 14); length of palatal bridge, 6.0 (0.4, 14); greatest depth (height) of rostrum, 13.6 (0.6, 14); parietal breadth, 24.2 (0.8, 14); and length of auditory bulla, 10.1 (0.4, 14—Chapman and Morgan 1973; Chapman et al. 1992).

DISTRIBUTION

Sylvilagus obscurus has a disjunct range across the southern Appalachian Mountains region from Pennsylvania to northern Alabama (Chapman et al. 1977; Chapman and Stauffer 1981; Chapman et al. 1992). Recent surveys indicate that the extent of the southern range is larger than previously reported (Campbell et al. 2010). The species range (Fig. 3) overlaps several physiographic regions: Appalachian Plateau, Blue Ridge, Interior Low Plateaus, and Ridge and Valley. S. obscurus is usually associated with high-elevation habitats (> 610 m), but numerous reports are from lower elevations too (Howell 1921; Llewellyn and Handley 1945; Paul and Quay 1963; Chapman and Paradiso 1972; Blymyer 1976; Fies and Coggin 1985; Chapman et al. 1992; Sole 1999; Hart 2001). Chapman and Stauffer (1981) suggested that S. obscurus and S. transitionalis are refugial relicts that became restricted to high-elevation sites as the climate warmed after the last glacial period.

FOSSIL RECORD

Pleistocene fossils from three sites discovered before Sylvilagus obscurus was named were designated as S. transitionalis, but perhaps represent S. obscurus because of their southerly location. Several complete and partial skulls were described from the New Paris sink holes in Bedford County, Pennsylvania (Guilday and Bender 1958). Skeletal fragments were reported from Clark’s Cave in Bath County, Virginia (Guilday et al. 1977) and at Ladds in Bartow County, Georgia (Lipps and Ray 1967). However, the assignment of these two fossil specimens to a species may be questionable, given that the osteological similarity between S. floridanus and S. obscurus makes specific identification of fragments, including of fossils, unreliable (Chapman and Morgan 1973).

FORM AND FUNCTION

The dental formula, like all other Sylvilagus, is i 2/1, c 0/0, p 3/2, m 3/3, total 28 (Whitaker and Hamilton 1998). Condition (measured as body mass/greatest length) for Sylvilagus obscurus in West Virginia and Maryland fluctuates throughout the year. Condition for both sexes increases from autumn to winter, remains steady through spring, and reaches its lowest point in the summer. Body fat deposits (qualitatively assessed) decline from winter to the spring/summer period (Chapman et al. 1977). The adrenal index (adrenal weight/body weight) for both sexes is significantly lower in the winter than the spring or summer, possibly because breeding occurs during the latter seasons (Chapman et al. 1977). Chapman et al. (1977) provide a detailed description of the histology and morphology of the reproductive organs.

ONTOGENY AND REPRODUCTION

Gestation is 28 days in Sylvilagus obscurus (Tefft and Chapman 1987). At birth, neonates have little fur and their eyes are closed, but they have rapid growth during their 16-day developmental period. By day 7, young begin to open their eyes and show coordinated movements. At day 13, young begin foraging, but return to the nest to rest; by day 16, they are fully independent with excellent coordination (Tefft and Chapman 1983). Data on reproduction are available for S. obscurus only from northern populations (Maryland and West Virginia), where breeding occurs from March to September with peak activity during March–July. Most females produce a first litter in March and April, with subsequent litters being produced later in the breeding season. A small number of females (< 20%) breed during their first year (Chapman et al. 1977). After parturition, the female immediately enters estrus and copulation follows, leading to the birth of the next litter about 28 days later (Tefft and Chapman 1987). Strong breeding synchrony is exhibited, with most females entering estrus around the same date, particularly at the beginning of the breeding season (Chapman et al. 1977; Tefft and Chapman 1987).

Ovaries of 14 females from West Virginia and Maryland had a mean ovulation rate of 3.7 eggs; about 30% of examined females had polyovular follicles, typically containing two eggs (range 1–4—Chapman et al. 1977). The average number of...
embryos in these females was 3.4. Females often produce multiple litters each year (seven of nine females in West Virginia/Maryland), with subsequent litters typically larger than first litters (4.0 versus 3.2—Chapman et al. 1977). In Maryland, a female in a natural enclosure produced three litters totaling 15 young during the breeding season (Tefft and Chapman 1983). Reabsorption of embryos is known only for the first litter (15% of known embryos, n = 14—Chapman et al. 1977).

Average testis weight of males increases dramatically over the breeding season (0.5 g in December to 3 g in April) and then declines after July, with a peak during March–July that coincides with female receptivity. Sperm does not reach substantial amounts in testes and epididymides until February, when average testis weight is 2 g. Males are not reproductively active until about 1 year old (Chapman et al. 1977).

**ECOLOGY**

Multiple studies from across its distribution indicate that dense woody understory is strongly associated with the presence of *Sylvilagus obscurus*. In Maryland, *S. obscurus* occupied dense early successional hardwood forests (<10-year-old regenerating clear-cuts) dominated by *Rubus allegheniensis* and mature mixed-oak forest with dense ericaceous shrub cover; steep slopes of more than 25° were avoided (Sommer 1997; Stevens and Barry 2002). In Maryland, home ranges had greater amounts of understory cover under 1.5 m compared to the surrounding habitat; at the microhabitat scale, *S. obscurus* preferred areas <2 m from concealment cover and <95% canopy closure (Stevens and Barry 2002). In West Virginia, *S. obscurus* occupied habitat with dense woody understory cover consisting of ericaceous shrub vegetation (*Kalmia latifolia*, *Rhododendron*, and *Vaccinium*) and coniferous stands (*Picea rubens*, *Pinus*, and *Abies balsamea*—Chapman and Morgan 1973; Boyce 2001; Sucke 2002). In Kentucky, 550 *S. obscurus* were collected by hunters from early successional forests often resulting from coal mine reclamation, timber harvesting, and farm abandonment (Sole 1999). In Pennsylvania, 89% of 120 *S. obscurus* captures were in dense scrub oak shrubland and the remaining ones were in bluestem savanna; none were captured in mixed oak forest, likely because this habitat lacked a well-developed understory (Holdermann 1978). In Tennessee, *S. obscurus* was associated with a mosaic of vegetation types that were dominated by early successional forest with *Rubus* cover (Laseter 1999). In Virginia, 20 individuals were captured primarily in 6- to 7-year-old clearcuts of early successional hardwood forest (Blymyer 1976). In South Carolina, 13 *S. obscurus* were captured in or adjacent to a 94-year-old pine stand with an ericaceous shrub understory (Russell et al. 1999). Additional captures have been reported in the following vegetation types: ericaceous shrub habitat in Kentucky (Barbour 1951), Alabama, and Georgia (Chapman and Stauffer 1981); pine-hardwood forest with hardwood sapling understory in Alabama (Hart 2001); 4-year-old coppiced forest in North Carolina (Gentry et al. 1968); and oldfield habitat in Maryland (Chapman and Paradiso 1972). In summary, *S. obscurus* uses a range of woody habitat types, but most have dense shrubs or saplings that provide both shelter and food.

Density of *S. obscurus* based on live trapping ranged from 0.2 to 0.7 individuals/ha in West Virginia (Sucke 2002). In Tennessee, density estimates ranged from 0.8 to 0.9 individuals/ha during winter (Laseter 1999). Based on monitoring of 44 rabbits in West Virginia, survivorship did not differ between sexes (daily survival rate = 0.99, monthly survival rate = 0.83, and yearly survival rate = 0.09). Subadults had lower monthly survival rates (0.51, n = 4) than adults (0.84, n = 40) but did not differ in daily or yearly survival. Survival rates were lower during the dormant season than in the growing season (Sucke 2002; Hartman and Barry 2010). Predation was the most frequent cause of death during a survivorship study in West Virginia (Sucke 2002). The sex ratio of adults varied among population studies, but is likely near 1:1; male:female ratios were reported as 32:56 (Chapman et al. 1977), 21:16 (Boyce 2001), and 24:20 (Hartman and Barry 2010).

*Sylvilagus obscurus* does not defend territories and often has considerable overlap in space use with conspecifics (Sommer 1997). Sexes show no strong differences in home range size, although space use does vary between seasons. In West Virginia, the mean 95% adaptive kernel home range for sexes combined was greater during the growing season (10 ha, n = 5) than the dormant season (4 ha, n = 14). Although females showed no seasonal differences, males had larger home ranges during the growing season (Boyce 2001; Boyce and Barry 2007). In western Maryland, median home ranges for males (n = 4) and females (n = 4) combined were 5.4 ha for 100% minimum convex polygon, 4.3 ha for 95% minimum convex polygon, and 4.7 ha for 95% adaptive kernel (Sommer 1997; Stevens and Barry 2002). Home ranges tended to end abruptly at the transitions to open areas, such as agricultural fields and mature forest lacking understory cover (Stevens and Barry 2002). Median distances moved per day by individuals (n = 14) in West Virginia ranged from 15 to 201 m. Median distance moved per day was greater for males than females during the growing season but distances were similar during the dormant season (Boyce 2001).

In western Maryland, the diet of *S. obscurus*, as determined by analysis of stomach contents, varied among seasons, with mostly woody material eaten in winter (> 85% of diet), but with grasses and forbs dominating during the other seasons (>70% of diet—Spencer 1985; Spencer and Chapman 1986). Consumed plants included the herbaceous species *Aster prenanthoides*, *Cryptotaenia canadensis*, *Dryopteris marginalis*, *Hieracium floribundum*, *Hieracium scabrum*, *Lotus corniculatus*, *Melilotus albus*, mosse, *Oxalis*, *Ranunculus acris*, *Smilacina racemose*, *Solidago*, *Spiranthes cernua*, and *Trifolium* and the woody species *Gaultheria procumbens*, *Rubus*, and *Smilax rotundifolia*. Fruits of hawthorn (*Crataegus*) are also eaten. Although *S. obscurus* can dig through deep snow to gain access to vegetation (Boyce 2001; Sucke 2002), during times of heavy snowfall it often relies on conifer needles from spruce (*Picea*) and eastern hemlock (*Tsuga canadensis*—Spencer and Chapman 2002).
Water is probably obtained from ingested vegetation because the drinking of free water has not been observed (Tefft and Chapman 1987). In a natural enclosure in Maryland, *S. obscurus* ate the bark of *Acer saccharum*, ferns, grasses, herbaceous plants (*Maianthemum canadense, Polygonatum biflorum, Smilacina racemosa,* and *Viola rotundifolia*), and woody plants (*Hamamelis virginiana, Rhus, Robinia pseudoacacia—Tefft and Chapman 1987*). Counts of clipped stems in West Virginia indicated that the most preferred woody plant species during winter were *Amelanchier, Lonicera,* and *Potentilla,* and to a lesser extent *Acer rubrum, H. virginiana, G. procumbens,* and *Vaccinium.* The most avoided woody plant species was *K. latifolia,* followed by *Rhododendron, Ilex montana, Nemopanthus mucronatus,* and *Viburnum Rubus* were neither preferred nor avoided (Sucke 2002; Hartman and Barry 2010).

Coprophagy is reported in many other species of the genus *Sylvilagus* and assumed to occur in *S. obscurus* as well (Chapman and Litvaitis 2003). Based on observations of *S. floridanus,* two types of fecal pellets are eliminated by cottontails: hard brown pellets and soft green pellets with a mucus coating (Bailey 1969). In leporids, hard pellets consist of poorly digested large food particles, whereas soft pellets are produced from food that has traveled through the cecum and undergone further digestion. As a result the soft pellets contain greater nitrogen levels (Bjornhag and Snipes 1999). Typically, the soft pellets are reingested, but there are reports of the hard pellets also being reingested in some leporids (Dirakawa 2001).

Ectoparasites include the ticks *Haemaphysalis leporispalustris* and *Ixodes dentatus* and the fleas *Cediopsylla simplex,* *Ctenocephalides canis,* and *Odontosyllus multispinosus* (Sonenshine et al. 1965; Harman and Chapman 1977). Bot flies (*Cuterebra*) infect *S. obscurus* (Harman and Chapman 1977; Jacobson and others 1978). Endoparasites include the flatworms *Cittotaenia variabilis* and *Taenia pisiformis* and the nematodes *Dermatoxys veliger,* *Obeliscoides cuniculi,* *Passalarius nonanulatus,* and *Trichostrongylus calcarares* (Holloway 1966).

Competition with *S. floridanus* is likely common throughout the range of *S. obscurus.* *S. floridanus* is a habitat generalist, thrives in human-modified habitats, and occupies many of the same areas as *S. obscurus.* Chapman and Morgan (1973) hypothesized that human-induced habitat modification and translocations have allowed *S. floridanus* to outcompete *S. obscurus* in many areas. Predators most likely include terrestrial and aerial species, including bobcat (*Lynx rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), weasels (*Mustela*), and raptors (*Boyce 2001; Sucke 2002*). Other causes of mortality include exposure from winter weather, hunting, and vehicular collisions (*Boyce 2001; Sucke 2002*). An eastern chipmunk (*Tamias striatus*) was observed attacking and wounding a juvenile *S. obscurus* (Odum 1949).

Survey techniques include live traps, hunter surveys, fecal-pellet counts, DNA analysis of pellets, and spotlight hunting (Laseter 1999; Sole 1999; Hart 2001; Hartman and Barry 2010; Adams et al. 2011). *S. obscurus* is typically captured with wooden box traps baited with apple slices (Hartman and Barry 2010). Individuals can be housed for extended periods in fenced, outdoor enclosures and fed commercial rabbit chow (Tefft and Chapman 1987).

**Behavior**

Tefft and Chapman (1983) provided extensive observations of the behavior of two male and one female *Sylvilagus obscurus* in a natural enclosure; the behavior described in this section is drawn from that study unless otherwise noted. Neither sex is territorial, but individuals show an affinity to particular areas (Tefft and Chapman 1987; Sommer 1997; Boyce 2001). Although individuals are typically solitary, they will interact in the course of daily movements and as females enter estrus. Females are often aggressive toward males, but sometimes a female forms a short-term consort relationship with a male between periods of estrus. Consort *S. obscurus* remain within 1–2 m of each other during their daily movements, but do not come in direct contact (within < 60 cm). As estrus approaches, females become more aggressive toward males and will not form consorts. Males develop dominant–subordinate relationships among themselves, often resulting in subordinate males avoiding dominant males. Dominant males sometimes dislodge subordinates by charging them; chases also occur, but fighting has not been observed in this species. As female estrus approaches, males become more aggressive toward other males.

Beginning 2–3 days before estrus, the female is highly aggressive toward males. On the day of estrus, the males pursue the female in a reproductive chase. Copulation occurs when one male rushes at a receptive female from the side or rear, mounts and clasps her side with his front legs, engages in 4–5 quick thrusts, and dismounts. After copulation, the sexes move away from each other and engage in self grooming and foraging behaviors. Females probably copulate with only one male per estrus. By 24 h after copulation, females become aggressive toward males again and social interactions between sexes decline.

One to two days before parturition, the female digs a burrow or a surface depression (i.e., a body-sized cleared area in dense vegetation or under a brush pile known as a “form”) as a nest site for newly born young. After the female gives birth, she nurses and grooms her young, and places them into the nest lined with fur pulled from her own body. When leaving the burrow, the female plugs the opening with fur and camouflage it by stamping leaves and twigs over the entrance. Females revisit the nest once a day to nurse the young, typically near dusk. Young of *S. obscurus* also are very secretive and do not show any play behavior or vocalizations.

Three vocalizations are known for *S. obscurus*; the tick-squel, squeak, and distress cry. The tick-squel, a chirping, clicking, or chattering call, is highly variable among individuals and typically is uttered during social and reproductive interactions. Dominant males use the tick-squel call toward subordinate males. The squeak is a high-pitched call performed...
during social interactions when individuals are excited or startled. The distress cry is a loud, high-pitched scream made by adults or young when threatened. Unlike other *Sylvilagus* species, no glandular scent marking has been reported. Fecal pellets are concentrated in latrines, which are situated in areas near where individuals spend significant amounts of time, such as at lookout posts or forms.

*Sylvilagus obscurus* is primarily crepuscular, with peak activity occurring before sunrise and after sunset. Individuals are cautious and secretive in nature, usually remaining in or near dense cover. *S. obscurus* develops well-worn paths that allow rapid escape when necessary. Even during periods of activity, movements are frequently interrupted by extended periods of stillness. During the day and periods of inclement weather, individuals rest in their sheltering forms. Foraging behavior usually consists of movements between dense clumps of vegetation, but *S. obscurus* also engages in grubbing and digging behavior to gain access to roots.

Stereotypic grooming behavior follows this sequence: 1) cleaning and licking of legs, feet, and hindquarters, 2) licking forepaws and using them to clean face and ears, and 3) licking and biting hindquarters, breast, and abdomen. When startled, *S. obscurus* sits alertly and freezes, followed by a direct line dash to cover if needed. If chased, it uses zigzag dashes to confuse pursuing predators. During warm periods, *S. obscurus* attempts to cool itself by panting and lying with limbs spread and venter in contact with the soil.

**GENETICS**

*Sylvilagus obscurus* has a diploid chromosome number (2n) of 46 and a fundamental number (FN) of 84 (Robinson et al. 1983; Ruedas et al. 1989). The chromosomes consist of 10 pairs of metacentric or submetacentric, 10 pairs of subtelocentric, and two pairs of acrocentric chromosomes, plus the pair of sex chromosomes. The X chromosome is medium size and submetacentric, and the Y chromosome is small and acrocentric (Robinson et al. 1983; Ruedas et al. 1989). Variation in serum proteins was minimal in *S. obscurus* from Maryland, and no polymorphisms were observed for 18 proteins (Chapman and Morgan 1973; Morgan and Chapman 1981). Chapman and Morgan (1973) describe a potential hybrid based on morphology between *S. obscurus* and *S. floridanus*. Mitochondrial DNA nucleotide diversity of six specimens was 0.177, and no hybridization with *S. floridanus* was detected (Litvaitis et al. 1997). The 12S ribosomal subunit gene contains a high percentage of adenine (>47%) in the loop regions (Halanych and Robinson 1997).

**CONSERVATION**

The International Union for Conservation of Nature and Natural Resources ranks *Sylvilagus obscurus* as “Near Threatened” (Barry and Lanier 2019). Of the 10 U.S. states in which *S. obscurus* occurs, conservation status classifications defined by NatureServe are as follows (Kentucky Department of Fish and Wildlife Resources 2013; Pennsylvania Game Commission and Pennsylvania Fish & Boat Commission 2015; NatureServe 2017): critically imperiled in Alabama and Maryland (S1), critically imperiled-to-imperiled in Georgia and Pennsylvania (S1, S2), imperiled in West Virginia and Kentucky (S2), vulnerable in North Carolina, South Carolina, and Tennessee (S3), and apparently secure in Virginia, but its rank there is uncertain (S4?). Major threats include habitat destruction and fragmentation caused by maturation of early successional forests and human development, climate change, and competition with *S. floridanus*, which requires less cover and thrives in developed areas (Chapman and Stauffer 1981; Yahner 2003; Barry and Lanier 2019; Gillen and Kiviat 2012).

**ACKNOWLEDGMENTS**

I thank Kelly Boyce, Kathy Boyle, Nikki Castleberry, Robert Dowler, Alana Hartman, Susan Klugman, Dianna Krejsa, Kris Light, James McCann, and Brian Streets for their technical assistance with this manuscript. Ronald Barry provided insightful comments that improved this manuscript.

**LITERATURE CITED**


Associate Editor of this account was ROBERT K. ROSE. Editor was MEREDITH J. HAMILTON.