History of Northern Saw-whet Owls (*Aegolius acadicus*) in North America: Discovery to present day

História do mocho-amolador (*Aegolius acadicus*) na América do Norte: desde a descoberta até ao presente

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ABSTRACT

The Northern Saw-whet Owl (*Aegolius acadicus*) is a small forest owl breeding throughout southern Canada and the mountains of the Unites States, including Alaska, and Mexico. It was first described from a specimen taken in Nova Scotia in 1791, but confusion existed for the next 100 years about its distribution; its relationship to its congener, the Boreal (or Tengmalm's) Owl (*Aegolius funereus*); and its juvenile plumage, which was described as belonging to a separate species. It also took many decades in the 20th century to establish its migratory and irruptive behavior in fall. A major breakthrough was the discovery in 1986 that saw-whets can be captured using audio lures during fall migration. They can also be sexed based on wing length and weight and aged based on ultraviolet patterns on their underwing. Since 1969, nearly 300,000 Northern Saw-whet Owls have been banded in North America, yet the winter distribution remains unclear, particularly in the southern United States and Mexico, and little is known about spring migration and the species' breeding biology. Here, we trace the complicated history of this species from discovery to the present.

Keywords: *Aegolius acadicus*, history, Northern Saw-whet Owl

RESUMO

O mocho-amolador (*Aegolius acadicus*) é uma pequena rapina noturna florestal encontrada no sul do Canadá e nas montanhas dos Estados Unidos, incluindo o Alasca e o norte do México, durante a época de reprodução. Foi descrito pela primeira vez a partir de um espécime proveniente da Nova Escócia em 1791, mas nos 100 anos seguintes não houve certeza sobre a sua distribuição; a sua relação com o seu congénere mocho-funéreo (*Aegolius funereus*); e a sua plumagem juvenil, que foi descrita como pertencente a uma espécie diferente. Também demorou várias décadas no século XX para conhecer o seu comportamento migratório e irruptivo no outono. Um grande avanço foi a descoberta, em 1986, de que os mochos-amoladores podem ser capturados durante a migração do outono através de atração por vocalizações conspecíficas. Podem também ser sexados com base no comprimento da asa e no peso, e a idade pode ser estimada com base em padrões de ultravioleta na parte interior da asa. Desde 1969, foram anilhados na América do Norte cerca de 300 mil mochos-amoladores, mas a sua distribuição no inverno ainda não está clara, particularmente no sul dos Estados Unidos e no México, e pouco se sabe sobre a migração de primavera e a biologia da espécie. Neste artigo descrevemos a história complexa desta espécie, desde a sua descoberta até ao presente.

Palavras-chave: *Aegolius acadicus*, história, mocho-amolador

Introduction

The Northern Saw-whet Owl (*Aegolius acadicus*) (hereafter saw-whet) is a small forest owl that breeds throughout most of southern Canada, northern United States including Alaska, coniferous habitats of the Appalachian Mountains in eastern United States, coniferous habitats of the Rocky Mountains in western United States, and south along the Cordillera into Mexico. Its winter distribution is poorly known, particularly in the southern United States, primarily due to it being nocturnal and usually silent in winter. Saw-whets are migratory and experience flight years, usually 4 years apart, when large numbers move south, due to increased nesting success when small mammal populations are high (Beckett & Proudfoot 2011, Henry et al. 2015). After it was discovered, in the 1980s, that migrating saw-whets respond to audio lures and can be captured in mist nests, banding stations began to proliferate in Canada and the United States.

Due to their secretive nature, few studies have been conducted on the breeding biology of saw-whets. It has been suggested that they are nomadic prior to breeding, typically do not nest in the same place year-to-year (low philopatry), and almost all young disperse from their breeding ground (Marks & Doremus 2000, Marks et al. 2015). Saw-whets are unusual among owls in that, for several months, juveniles have a plumage that looks nothing like the adult plumage.

Here we trace the species' discovery, including early confusion with its congener, Boreal Owl (*Aegolius funereus*); description of juveniles as a new species; the debate during the first half of the 20th Century about whether saw-whets were migratory; and recent advances since the introduction of audio lures in the 1980s.

Figure 1 - Acadian Owl (bottom left) from Latham (1781). Based on a specimen shot by a British officer in the 1770s, while on tour of duty in Nova Scotia during the American Revolution.

Figura 1 - "Mocho acádico" de Latham (1781). Baseado num espécime filmado por um oficial britânico na década de 1770, durante uma missão na Nova Escócia durante a Revolução Americana.

1781-1862

The first mention of saw-whet appeared in the first volume of *A General Synopsis of Birds*, written by Latham (1781). His painting of the species is less than realistic, based on both a dead specimen and a sketch from Captain Thomas Davies, but it is apparently of a saw-whet nonetheless (Fig. 1). Davies was an officer in the British Army, a naturalist, and talented painter who had a passion for painting landscape scenes, people, and nature. Davies was twice stationed in Halifax, Nova Scotia during the early years of the American Revolution and likely collected the specimen then, which Latham dubbed "Acadian Owl". Latham's (1781) written description of this owl is as good as any, capturing all the highlights of an adult saw-whet.

Not given a Latin name by Latham (1781), Acadian Owl is mentioned again by Gmelin (1788), who published an official account to name the species in the 13th edition of Linnaeus' *Systema Naturae*. The saw-whet remained commonly known as Acadian Owl, but now had its first binomial Latin name: *Strix acadica*. Little was written about the species in Gmelin (1788), but it was based on Latham's (1781) description. Various other naturalists gave accounts of Acadian Owl around the turn of the 19th-century. A description of "Chouette d'Acadie" or, *Strix acadica,* made a brief appearance in Daudin (1800). However, problems arose in several other volumes. Pennant (1785) mentioned a species called Little Owl (*Strix passerina*) as being common from Hudson Bay to New York, as well as frequent in Russia and occasional to Siberia. He cited Latham's 1781 account of *Strix acadica,* but a range to Russia and Siberia raises a red flag. Pennant (1785) noted a size variation of 7 - 8 inches (18 -20 cm) in length, stating "the smallest I have seen is from Nova Scotia; which has white circlets about the eyes, and fewer white spots on its plumage". Almost certainly, Pennant was referring to a saw-whet in this part of his account. However, the range he gave and a description of the bill being "whitish brown" suggests Boreal Owl.

Wilson (1811) seemed similarly confused. In his account of Little Owl, again listed as *Strix passerina*, he noted the species as being "…a general and constant inhabitant of the middle and northern states…found as far north as Nova Scotia, and even Hudson's bay…", but also as frequent in Russia. In size, the author noted a length of 7.5 inches (19 cm) and an "extent" of 18 inches (46 cm). He also mentioned a blackish, horn colored bill, a feature the Boreal Owl lacks. Despite the described range, all other notes by Wilson seemed to match that of saw-whet, rather than Boreal Owl. His illustration of the species is very clearly a saw-whet and is of a specimen shot near Great Egg Harbor in New Jersey (Fig. 2).

It seems likely that both Pennant and Wilson believed Boreal Owl and saw-whets to be conspecific. Latham (1821) listed both Acadian Owl (*Strix acadiensis*) and Little Owl (*S. passerina*) as separate species; however, ranges of the two were still muddied by nonexistent overlap into northern Europe. Latham wrote that Acadian Owl was an inhabitant of North America, mentioning again the specimen collected by Davies some 40 years earlier, but he also described the species as occurring in the mountainous regions of Germany. He believed Little Owl was common throughout various regions of Europe and India, but also around Hudson Bay in Canada.

In addition, Bonaparte (1828), ornithologist and nephew of Napoleon Bonaparte, confused ranges of the two owls. He remarked that *S. acadica* occurs in "the north of both continents, but [is] more common in America, in the northern and middle states…" He cites Wilson's Little Owl as a visual complement to his brief account.

It was not until Swainson & Richardson (1831) that the issue was resolved. This work encompassed multiple volumes filled with

Figure 2 - Wilson (1811) was accurate in his illustration but mistook part of the range for that of the Boreal (Tengmalm's) Owl.

Figura 2 - Wilson (1811) foi preciso na sua ilustração mas confundiu parte da área de distribuição com a do mocho-funéreo.

fauna documented during two separate expeditions through northern Canada, led by Sir John Franklin. John Richardson was brought on as surgeon and naturalist during the first expedition (1819-1822) and again for the second expedition (1824-1827). He was assisted by William Swainson and Thomas Drummond. Natural history was not the primary aim of the expeditions and none of the trio were ornithologists. However, they successfully documented 240 avian species during the expeditions, with accounts of 27 others based on the writings of their predecessors (Swainson & Richardson 1831).

At the beginning of the second volume on birds, Swainson & Richardson (1831) addressed Pennant's mistakes: "…unaccompanied by specimens, prefixing the names of nearly-resembling European birds, which an actual comparison would have shown to have been quite distinct; and in this way several species have been enumerated in systematic works as natives of Hudson's Bay, which do not actually exist there." They went on to say, "in common with other ornithological works of that period, it [*Arctic Zoology*] includes many specific names, attached merely to a different state of plumage resulting from age or sex."

Swainson & Richardson (1831), for what appears to be the first time, listed *S. acadica* and *S. passerina* as two distinct species, with none of the former confusion as to range and physical appearance. Accounts for both species were quite detailed and noted differentiating features of plumage and size. In their account of *S. acadica*, which they termed "American Sparrow Owl", Wilson's *S. passerina* was confirmed with "no doubt" to be *S. acadica*. As for Pennant, they stated "… it is impossible to ascertain what particular bird the author had in view. It appears highly probable that he considered the two American species, with another found in Sweden to be mere varieties…" The naturalists of the Franklin expedition did not encounter *S. acadica* on expedition routes, but obtained two specimens from New Caledonia, in present day British Columbia (Swainson & Richardson 1831).

Audubon (1831) beautifully illustrated the Little (Acadian) Owl *S. acadica* as its own species for the first time (Fig. 3) and did the same for Tengmalm's Owl (*S. tengmalmi*) seven years later (Audubon 1838). The plates and descriptions of both species are stunning and accurate. Audubon's accounts for each were written in pleasing flowery, if not exaggerated prose, typical of the naturalist. He encountered *S. acadica* during some travels in the eastern states, purportedly finding nests as far south as Louisiana and Natchez (southwestern Mississippi). This has great potential for inaccuracy, as these saw-whets would have been much farther south than is typical during the breeding season today. He went on to note the species as breeding in greater abundance in the northeastern United States, where it is commonly encountered. Audubon mentions *S. acadica* as occurring farther south than *S. tengmalmi*, an accurate observation.

During a time when naturalists commonly conducted their own work with little collaboration, it would only be natural for there to be some continued confusion over *S. acadica*. It is difficult to determine what Nuttall (1832) made of *S. acadica*, other than it was separate from Wilson's *S. passerina* and *S. tengmalmi*. This is interesting, because between Wilson (1811) and Nuttall (1832), *Strix passerina* appeared to fall out of use in favor of *S. tengmalmi*. Nuttall (1832) began his account with a comment about *S. acadica* being an inhabitant of the northern portions of North America and Europe. He went on to say the species rarely wandered from northern Europe, whereas in North America, it was common farther south to New Jersey and Pennsylvania. Though not the same species, the account of range is somewhat accurate, as Tengmalm's (Boreal) Owl is not migratory, but irruptive in northern Europe. Saw-whets are migratory, explaining *S. acadica*'s occurrence farther south in North America. Nuttall's species description fits that of

Figure 3 - *S. acadica*, fearsomely illustrated in Audubon's Birds of America: Vol. 2 (1831).

Figura 3 - Ilustração de *S. acadica* com aspeto assustador em Audubon's Birds of America: vol. 2 (1831)

saw-whets. He closed his account with a note of personal communication with Bonaparte: "…in a letter to W. Cooper, Esq. says, he [Bonaparte] has recently ascertained that this species differs from all the other European small kinds of the genus". So why write such a bewildering account?

Up to this point, the saw-whet had been known by its first Latin name, *Strix acadica*, but that was changed by Bonaparte (1838). Bonaparte lived in America only a short time to complete Alexander Wilson's *American Ornithology*, after which he returned home to Italy and completed his own work in 1838, giving the saw-whet its second Latin name, *Nyctale acadica*, after the splitting of genus *Strix*.

The usage of *Strix acadica* materialized again when Gray (1844) compiled a *List of the Specimens of Birds in the Collection of the British Museum*. He also used *Glaucidium passerinum* for Little Owl, citing Linnaeus, Temminck, Daudins, and several others. However, with specimens from Germany and present-day Slovenia, it seems unlikely Gray was referring to the North American species. Another Latin name for the Acadian Owl, *Ulula acadica*, appeared in two publications (de Kay 1844, Giraud 1844), but did not gain popularity.

By 1860, expansion into western territories was increasing our knowledge of the saw-whet's range. In 1858, Spencer Baird, John Cassin, and George Lawrence, under direction of Secretary of War, Jefferson Davis and the Smithsonian Institution, were tasked to compile species accounts for bird specimens collected during railroad expeditions of the early 1850s, listing *N. acadica* as "the smallest owl found in the eastern and middle States of North America" (Baird 1858). Based on specimens from the expeditions, they also reported it as a likely resident of the "entire temperate regions of this division of the continent", as well as being found in California. Two specimens were collected by Suckley: one near Fort Dalles, Oregon Territory on 7 December 1853 and the other near Fort Vancouver, Washington Territory on 3 February 1854 (Cooper & Suckley 1860). A third specimen was collected in Texas by Captain John Pope, leader of the "Far Southern Route", which explored the possibility for a railroad along the 32nd parallel. Pope's party travelled east from El Paso to the Red River Valley from January to May 1854. Another saw-whet reportedly collected in Fort Smith, Arkansas, in July 1853 by the Whipple Expedition has been largely dismissed (see Pruitt & Smith 2016).

Gradually, the natural history of the saw-whet became much more transparent than it was for nearly 100 years. Cassin (1862) wrote that *N. acadica* was found in "the whole of North America". He cited several sources to aid in drawing this conclusion, including Townsend (1839, Oregon), Gambel (1846, California), Audubon (1831, Kentucky and Louisiana), Kirtland (1838, Ohio), and Hoy (1852, Wisconsin).

The Mystery of the White-fronted Owl

During the time that genera *Strix* and *Nyctale* were being sorted out, an old taxonomical error resurfaced. This originated in the late 18th century when Shaw & Nodder (1789) described the White-fronted Owl (*Strix albifrons*), which surfaced again in Latham (1801), with a specimen collected in Quebec by Thomas Davies in 1790. Latham (1801) described the owl as having upperparts of dark brown, white around the eyes, extending down from the lower mandible, as well as white speckling on the wings and tail. The bird's breast and throat were a ruddy chestnut. Based on Latham's note of the owl "frequently erecting two feathers over the eye", Vieillot (1807) classified the species with eared owls. He proposed the possibility of "le hibou a front blanc", being a juvenile form of the red-eared owl (*Bubo asio*), today's Eastern Screech-Owl (*Megascops asio*).

German zoologist Lichtenstein (1838)

delved deeper after receiving specimens collected along the west coast of America. After addressing the mix-up between *Strix acadica* and its European counterparts, he went on to comment about *Strix frontalis* (the Latin name he used for White-fronted Owl). He stated (in German) that "Latham's *Strix acadica*… [is] nothing more than the immature plumage of our *Strix frontalis*". To be clear, when Lichtenstein referred to adults, he was picturing chocolate-brown *S. frontalis* and when he referred to juveniles, he was picturing a typical-looking adult of *S. acadica*. He supported this hypothesis with an interesting idea. Several specimens obtained came from eastern North America and were in "immature" plumage, really the adult plumage of *S. acadica*; others, collected in California, were dark brown "adult" specimens. He concluded the west must be within the owl's resident range and "immature" birds migrate to the eastern part of the continent. Lichtenstein came closer to an accurate conclusion than any naturalist before him but was still wrong. He was correct in believing a relationship between *S. frontalis* and *S. acadica* but was incorrect in his order of operations. The cocoa-and-buff-colored birds dubbed *frontalis* are, in fact, immatures of *acadica*. However, misclassification would continue for over 30 years.

Hoy (1852) re-described White-fronted Owl as *Nyctale kirtlandii*. One cannot be sure, but it is feasible Hoy had never seen Lichtenstein's (1838) paper. According to Hoy (1852), this species is of similar size to *Nyctale acadica*, but colored quite differently. Specimens used by Hoy in his description include a bird captured in October 1821 and another collected in July 1852.

Three years later, Strickland (1855) authored *Ornithological Synonyms*, a book he hoped would combat the problem of synonymy in scientific naming, which had become a dilemma for ornithologists working around the world. An Englishman, it is plausible Strickland was in contact with or had obtained Lichtenstein's (1838) paper. As a result, he placed *S. albifrons*, *S. frontalis*, and several other names for White-fronted Owl on the list of synonyms for *N. acadica*, which was still the official species name.

In America, classification of *N. kirtlandii* was further supported by Cassin (1862) with a lengthy description and a plate in his guide (Fig. 4). He briefly noted resemblance to Lichtenstein's *S. frontalis* but said nothing more and identified Hoy (1852) as first to describe *N. kirtlandii*. Cassin stated it to be an uncommon species, observed during the breeding season and winter, assuming it to be a resident in its range. Knowing typical immature saw-whets have completely molted into adult plumage by mid-September (Weidensaul 2015), Cassin's winter records were probably based on often-inaccurate written or verbal accounts with no supporting specimens.

N. kirtlandii continued to be supported by various ornithologists until Ridgway (1872) wrote a response to a paper published just months earlier by Elliot (1872), who compared adult and immature *Nyctale tengmalmi* (Boreal Owl) to *N. kirtlandii*. Elliot concluded that, given size and plumage similarities of immatures of both species, individuals of the so-called *N. kirtlandii* are really immatures of *N. tengmalmi*. In his analysis, Elliot also compared adults of *N. tengmalmi* from Europe and *N. richardsonii* from North America, concluding these species (eventually Boreal Owl) are conspecific.

In response, Ridgway (1872) addressed Elliot's changes, disagreeing with his placement of *N. kirtlandii* as immature individuals of *N. tengmalmi*. Ridgway stated that *N. kirtlandii* was identical in many aspects to *N. acadica* and, being little more than half the size of *N. tengmalmi*, cannot be conspecific with the latter. He countered Elliot's argument by proposing *N. kirtlandii* to be the young of *N. acadica*, providing five reasons why he believed this to be so, based on his examination of specimens from the Smithsonian Institution: (1) all specimens of *N. kirtlandii* are clearly immature birds; (2) all specimens of

N. acadica are clearly adult birds and there is no description of the species' young; (3) the ranges of both "species" are the same, as are some plumage characteristics, both having white "scalloping" on the alula, similar location and number of white bars on the tail and similar white spots on the primaries; (4) one of four *N. kirtlandii* specimens was an extremely dark individual exhibiting a facial disk of uniform brown and lacking spots on the forehead, likely a very young bird; and (5) three of four *N. kirtlandii* specimens exhibited a white-and-brown streaked facial disk and a streaked forehead, similar to that of adult *N. acadica*, likely older juveniles that had already begun molting into adult plumage. Ridgway (1872) ended by stating that those five facts "point conclusively to the identity of the *Nyctale 'albifrons'* [kirtlandii] and *N. acadica*."

Turn of the Century Developments

Perhaps because of Ridgway's paper, Coues (1872) listed the several names given to juveniles as figments of the past, settling into the usage of Acadian Owl (*Nyctale acadica*), and his text was among the first to use "Saw-whet Owl" as a major common name. The updated range in his book showed saw-whets to occur in the United States, north into Canada, and south into Mexico. *N. acadica*'s presence in Mexico was described, with little more detail, in Cooper (1870) as ranging to Oaxaca in southern Mexico.

Knowledge of the saw-whet's range continued to expand around the turn of the 20th century. Documentation of breeding birds in the central Sierra Nevada Mountains (Ray 1903), Arizona (Mearns 1890), and Colorado (Cooke 1897) widened the saw-whet's distribution down the Rocky Mountain Cordillera into Mexico. Its Mexican range was expanded in Salvin & Godman (1904), though the species was noted as uncommonly encountered. Two specimens existed at the time of publishing, an old specimen from Oaxaca and a more recent one from Chimalpa. In addition, the authors mentioned a specimen collected near Quetzaltenango, Guatemala. They noted this bird resembled the young brown plumage of *N. acadica*. However, it was most likely that this specimen was an Unspotted Saw-whet Owl (*Aegolius ridgwayi*), a new species that would be described by Alfaro (1905).

From the late-1870s through the 1890s, accounts of breeding and/or nesting saw-whets began to appear. One of the first well-documented accounts of juveniles being captured at breeding sites came from Massachusetts during summer 1876. The account described three encounters, including one individual captured by an inmate in his cell at the Deer Island Prison, near Boston (Deane 1877).

Massachusetts' saw-whets continued to impress the ornithological community with the acquisition of a full set of eggs from Tyngsboro in April 1881. Brewster (1881) stated that prior to the collection of this clutch, a single egg at the National Museum in Washington was the only known example. Brewster excitedly received the eggs along with both adults, which had attended the nest. Several months later, Brewster's contact from Tyngsboro sent him four nestling saw-whets. Brewster prepared three as specimens and raised one to adulthood, publishing a detailed narrative of its molt into adult plumage. In so doing, he confirmed the combination of *N. kirtlandii* and *N. acadica*, whose molt had never been documented. By the first of September, the immature bird "had become a remarkably beautiful Saw-whet Owl" (Brewster 1882).

Saw-whet eggs were first depicted in Bendire (1892), who expressed the importance of recent breakthroughs in nesting habits of the saw-whet, describing many accounts of nesting in both the eastern and western United States during the decade prior to publishing his book.

As reports of breeding and nesting saw-whets were being published, a variety of

names for the species remained in use. In September 1883, the American Ornithologists' Union (AOU) was formed to aid the development of ornithology and bird conservation in North America. The AOU also took over official taxonomy of American birds. In the first edition of the *Check-List of North American Birds* (AOU 1886), genus *Nyctale* was replaced with *Nyctala*, but the two were used interchangeably in the last decades of the 1800s. Also, in that checklist, the common name was officially changed to Saw-whet Owl; afterwards, the usage of "Acadian Owl" would fade away. A new genus name, *Cryptoglaux* ("hidden owl"), was proposed by Richmond (1901) and received the AOU's seal of approval in the 11th supplement to the 2nd second edition *Check-List* (AOU 1902). The change was necessitated by the occupation of the name *Nyctalus* for a genus of mammals. In the 14th supplement to the 2nd edition (AOU 1908), the genus *Cryptoglaux* was briefly shortened to *Glaux*, but was returned to *Cryptoglaux* in the 3rd edition of the checklist two years later (AOU 1910).

In 1901, just before *Nyctala* was removed as an avian genus, a putative subspecies to the saw-whet was described by Osgood (1901) based on a single specimen collected by John H. Keen 12 December 1896, on the Queen Charlotte Islands (now Haida Gwaii), British Columbia, Canada. Osgood detailed his *Nyctale acadica scotaea* as similar to *N. acadica*, but with all markings decidedly darker. He remarked that, during his 1900 expedition to the islands, a single individual flying over their anchored boat was the only saw-whet seen, and no specimens were collected. However, Osgood was generous in concluding the new owl must be common along the "humid Pacific coast". The subspecies *N. a. scotaea* was officially adopted in the 11th supplement to the 2nd edition of the *Check-list* (AOU 1902). It saw the same name changes as the nominate subspecies. With the new subspecies came the need to identify saw-whets found throughout the rest of North America. In the 3rd edition of the AOU checklist (1910), *Cryptoglaux acadica acadica* became the name to complement the range-limited northwestern subspecies.

Ridgway (1914) was skeptical of *C. a. scotaea* and Osgood's single referenced specimen, refusing to accept it as anything more than an individual with a color aberration. He wrote that he was "of the opinion that these characters will not prove constant when more specimens from the Queen Charlotte Islands have been examined". It was determined the plumage aberrations noted by Osgood were not far off from variant forms of nominate *C. a. acadica* from elsewhere in North America. Lack of support led to the removal of the subspecies from the 1916 AOU checklist (Sealy 2013). Supported by a collection date of 12 December, it has been proposed the original *C. a. scotaea* specimen was an individual of *C. a. acadica,* an occasional migrant to the islands (Brooks & Swarth 1925). Seasonal presence of the nominate subspecies on the islands during non-breeding season was not well documented until later (Withrow et al. 2014). Two years later, Fleming (1916) compared many specimens of saw-whet from across North America to four he obtained from Haida Gwaii, as well as the *C. a. scotaea* specimen. He concluded the four Haida Gwaii individuals were very different from both the mainland *C. a. acadica* and Osgood's *C. a. scotaea*, making note of extensive dark, reddish browns. Fleming ended his account with a motion to rename the four Haida Gwaii specimens *C. a. brooksi*, after renowned ornithologist and painter Allan Brooks. The Latin name, accompanied by the common name "Island Saw-whet Owl" was officially accepted in the 18th supplement to the AOU checklist (1923). Eventually, the subspecies status of *brooksi* was confirmed by genetic analysis, likely diverging around 16,000 years ago (Withrow et al. 2014).

The genus of the saw-whet would remain *Cryptoglaux* until it was changed to its current *Aegolius* in the 22nd supplement to the 4th edition of the *Check-List* (AOU 1947) based on Kaup's (1829) usage. The subspe-

cies epithet of *A. a. acadica* was changed to *A. a. acadicus* and adopted as the species epithet several years later, leaving the Latin name as *Aegolius acadicus*. The common name, "Northern Saw-whet Owl", was officially accepted in the 34th supplement to the *Check-List* (AOU 1983).

A New Age of Saw-whetting: Migration

In early accounts, saw-whets were rarely listed as common or abundant. For years, most authors did not mention seasonality, unless it was in respect to the Kirtland's Owl, which was suspiciously found only during summer or early fall. Today, saw-whets are known to be both regularly migratory and "irruptive" on roughly four-year cycles (Henry et al. 2015). Irruptions occur in autumn following a very successful breeding season when there are more individuals in the population, resulting in a heavier southward migration (Brittain et al. 2009). Most of this knowledge would not come until much later.

Possibly the earliest mention of saw-whet seasonality was made by Snow (1873), who stated simply that saw-whets are rare migratory visitors to Kansas. He provided no more information, so how he came to this conclusion cannot be determined. Langdon (1879) added to the suspicion of seasonal movements, citing the collection of three specimens and concluding saw-whets to be rare winter visitors in the Cincinnati, Ohio area. More accounts of saw-whets as "rare winter visitors" emerged in the latter part of the 19th century. Several reports came from Washington, D.C.: one ornithologist described seven autumn encounters with the species (Webster 1887) and five saw-whets were taken during winter of 1890-1891 (Hasbrouk 1891). If irruption years have held true to roughly four-year cycles, 1890 may have been an irruption. In the same decade, wintering birds appeared in coastal Virginia (Rives 1890) and coastal North Carolina (Brimley 1893), neither location within the known breeding range. Bendire (1892) acknowledged that saw-whets migrate from the northern breeding range to winter in the "Middle States", where they are often found "in considerable numbers". He cited W. E. D. Scott, who collected 21 specimens in December 1878 in New Jersey. This record, and others, led Fisher (1893) to his partially correct deduction in calling the owl an "irregular wanderer", seeking food in fall and winter. Such a large number collected, and timing of irruption cycles could point towards 1878 having been another irruption.

Reports of autumn and winter records continued into the 20th century, some from the central U.S., with saw-whets being captured or collected in Indiana (Ulrey & Wallace 1895), Cleveland, Ohio (Jones 1906), and Iowa (Wilson 1906). Jones (1906) stated the species was common in the vicinity of Cleveland in late fall and winter. The story is similar in Iowa, where Wilson (1906) listed it as rare in winter, with records from February 1889, April 1890, and March 1891.

In the East, more winter records outside the saw-whet's normal breeding range were reported. A female was captured alive near Weston, South Carolina on 11 November 1909 (Wayne 1911), whereas another female was collected near Tybee Island, along the northern coast of Georgia on New Year's Day 1911 (Hoxie 1911). These records set the stage for future autumn migration studies throughout eastern and central North America.

Perhaps the most interesting observation of the saw-whet's mysterious seasonality was made by Saunders (1907) and Taverner & Swales (1911). Saunders chronicled a "migration disaster" along the shores of Lake Huron near Port Franks, Ontario. During a large winter storm in October 1906, birds undergoing a "heavy migration" never made it across the lake, washing up in the following days by the thousands. Saunders arrived at the site on 21 October to find 1,845 carcasses along several km of shoreline. Among the dead were 24 saw-whets. At the time, this species was considered rare in western

Figure 5 - Photo taken by Percy A. Taverner at Point Pelee, 15 October 1910. Featured on the cover of *Canadian Geographical Journal* in 1938.

Figura 5 - Fotografia da autoria de Percy A. Taverner tirada em Pont Pelee em 15 de Outubro de 1910. Capa do *Canadian Geographical Journal* em 1938.

Ontario. Saunders speculated that saw-whets might migrate "in considerable numbers".

Taverner & Swales (1911) documented an earlier event, an anecdote from passengers on the steamship *Helena*. While the ship was near Little Duck Island on Lake Huron, passengers noticed a large evening migration of small owls fitting the description of saw-whets, some of which reportedly landed to rest on the ship's deck during the night.

The authors' premise was that saw-whets probably migrate more extensively than believed. On 30 October 1908, while working in the cedar thickets at Point Pelee on the north shore of Lake Erie, Swales discovered fresh remains of two saw-whets that he suggested could have been taken by a Cooper's Hawk (*Accipiter cooperii*). Two years later, on 15 October 1910, Taverner found the remains of another saw-whet in the same thicket. It was not long before the two captured a live bird perched near the ground; nearby another was feeding on a mouse. In under two hours, the authors found 26 saw-whets. Returning to camp for a camera, they eventually managed to photograph one (Fig. 5). Along with saw-whets, Taverner & Swales (1911) found six Long-eared Owls (*Asio otus*) and two Short-eared Owls (*Asio flammeus*). No owls of any species were found the next day. They remarked that similar counts of saw-whets had been found about 96 km east at Long Point, Ontario. Their contacts there told how saw-whets could be captured by spanning gill nets, typically used to catch fish, across woodland roads in fall. Evidently, enough owls were caught in this manner to render the outrageous story believable. Taverner & Swales (1911) close with a statement that would eventually be proven: "… the close tallying of all the dates point to the conclusion that from the middle to the end of October the Saw-whet Owls migrate in considerable numbers…".

One of the earliest documented bandings of a saw-whet occurred in March 1928. An owl was found during the day near a banding station in Cohasset, Massachusetts and, after a chase, was captured in a butterfly net (Harding 1929). Another banding report in November 1929, was of a bird captured at the Stone Bird Sanctuary in Babson Park, Massachusetts. The bander captured it in an insect net (Smith 1930).

During the 1930s and 1940s, extensive autumn banding occurred around Toronto, Ontario. Lambert (1949) wrote a brief statement summarizing 15 years of owl banding 1934-1948, during which their group banded over 200 individuals. Their passive methods involved simply erecting mist nets in areas that seemed good for capturing the birds, which usually included clearings, woodland edges, and woodland trails, small open areas where a saw-whet might be hunting. Initially, they averaged 1-3 owls per year between 1934 and 1938, then 18-25 owls per year from 1939-1947, and an unprecedented 62 owls in 1948. If the roughly four-year cycles of irruption have held true over the last 70 years, 1948 could have been an irruption year.

Capturing saw-whets for banding was attempted again on 18 October 1958 at Point Pelee, about 320 km west of Toronto. Eight mist nets were set that night and three saw-whets were captured. This meager number was enough to spur the Ontario Bird Banding Association (OBBA) to start a long-term banding project for the species. Around the same time, disagreement over the ethics of bird banding caused Point Pelee National Park to restrict operations, leading the OBBA to move much of its banding east along Lake Erie to Long Point. By 1973, all banding, other than that conducted in support of a specific study, was ceased at Point Pelee. One of the first projects to be approved after the enactment of research restrictions was a saw-whet migration study (O'Neill 2006).

Both Point Pelee and Long Point are peninsulas jutting into Lake Erie and are prime locations for banding operations. These features create a funnel for migrants that travel overland as long as possible before making the potentially costly lake crossing into the United States (Woodford 1959). Examples

of "peninsular effect" can be found around the world, especially for raptors, which are particularly cautious of making long-distance water crossings (Bildstein 2006).

While the shores of Lake Erie were early sites of saw-whet banding, the secretive owl was being captured elsewhere. On 6 November 1960, Walkimshaw kept his mist net open during the night to save time setting up the following morning at Battle Creek, Michigan. Just before daylight, he examined the net in his backyard and discovered a saw-whet. Over five years, Walkimshaw (1965) captured ten in similar manner, all in mid-October except for one November bird.

Further west, near Milwaukee, Wisconsin, the Cedar Grove Ornithological Station (CGOS) was also leaving nets up through the night to avoid extra work early in the morning. In 1956, they captured their first saw-whet in this way. By the end of the 1961 field season, 45 saw-whets had been captured in September and October. In fall 1962, CGOS researchers broadened their netting repertoire and range to include more nets with a larger mesh size spread out over a wider area (Mueller & Berger 1967). The group averaged 53 nights afield from 1962 to 1964 (September to November) and captured 168 saw-whets. The latter two years of the study saw a more than doubling of the 1962 capture rate. Based on the roughly four-year irruptive cycles, 1964 could have been such a year.

According to some sources, autumn 1965 may have been an irruption year as well. Birders and banding stations in Ontario and the northeastern U.S. documented 400 encounters with saw-whets: 285 of these were banded from September to December, whereas the others were seen by observers or found dead. Saw-whets were captured at banding stations at Long Island, New York, Massachusetts, and Toronto. Others were documented in Rhode Island, New Jersey, West Virginia, and northern Florida. One owl even roosted on a tractor engine in a Pan American hangar at Kennedy International Airport in New York (Davis 1966).

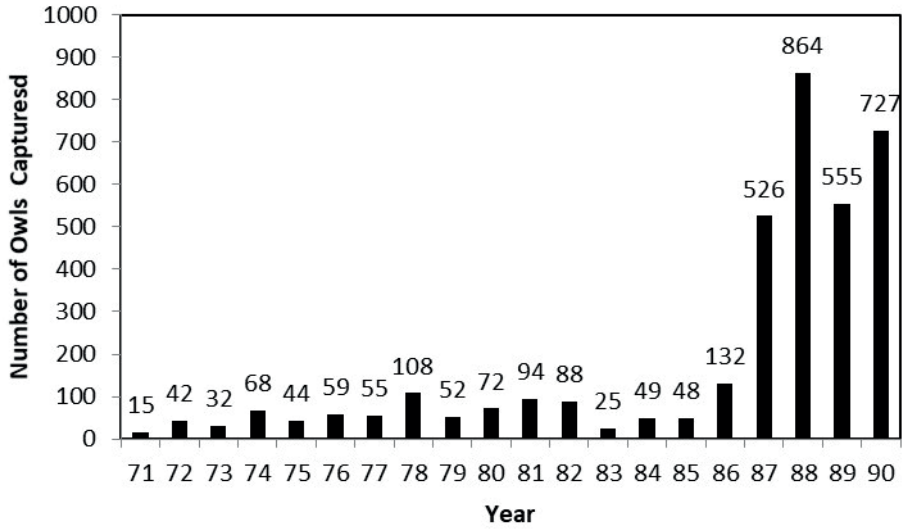
Holroyd & Woods (1975) summarized banding data from 1955 to 1969, the first period where a greater effort was put into capturing saw-whets. During this time, 4,802 saw-whets were banded in North America, 92% east of the Mississippi River. By far, early fall banding efforts were centered in southwestern Ontario, along the northern shores of Lake Erie and Lake Ontario. At this time, researchers in Wisconsin, Michigan, New York, New Jersey, and Maryland also banded their fair share of saw-whets. The authors acquired data on 52 band recoveries, leading them to suggest the existence of two major migratory pathways: one encompassing the Ohio and Mississippi River valleys, the other along the Atlantic Coast from Maine to North Carolina. Both pathways continue to be recognized.

A study conducted at Prince Edward Point, Ontario from 1975 to 1978 further demonstrated the apparently easy work of capturing saw-whets during fall migration, even using passive netting methods popular at the time. A total of 1,128 saw-whets was banded during those 3 years. Based on weather data from Prince Edward Point, they demonstrated that saw-whets were captured most often on calm, clear nights following the passage of a cold front (Weir et al. 1980).

By the early 1900s, there was no longer any question as to the migratory habits of saw-whets but capture methods had not been perfected to maximize captures for the amount of effort spent in the field. The major downfall to using passive netting techniques on a secretive migratory owl was that a banding station needed to increase the number of mist nets to increase capture rates. Raising many nets in hopes a saw-whet might fly in left much to chance. This became burdensome for many stations, either from lack of funding or personnel, which is why the introduction of the audio lure in 1986 was such a monumental development. Audio lures for saw-whets were first used at the Little Suamico Ornithological Station (LSOS), near Green

Figure 6 - Use of audio lures started in Wisconsin in 1986 and dramatically increased the number of saw-whets captured in fall migration (redrawn from Erdman & Brinker 1997).

Figura 6 - O uso de atração por vocalizações conspecíficas teve início no Wisconsin em 1986 e aumentou muito o número de mochos-amoladores capturados na migração de outono (redesenhado a partir de Erdman & Brinker 1997).



Bay, Wisconsin, and consisted of a cassette tape player, an amplifier, and two weather-proof speakers attached to a power supply. The species' solicitation call was broadcast into the night on a continuous loop. The distance at which this call could be heard was nearly 2 km. From 1971 to 1985, LSOS operated using passive netting techniques and captured an average of 57 individuals each fall, ranging from 15 in the least productive year to 108 in the most productive year (Fig. 6). In the audio lure period, 1986 to 1995, average number of captures per year jumped to an incredible 636, ranging from 526 in the least productive year to 864 in the most productive year (Erdman & Brinker 1997). The results, replicated at two sites in Maryland, were staggering and audio lures became standard protocol for saw-whet researchers across North America.

A concern with audio lures is the potential bias it introduces to the sex ratio of captures. The male's solicitation call is the most charismatic of the saw-whet's sounds, making it a natural choice for audio lures, but broadcasting a male-only call may create female-bias. This was demonstrated during a spring migration study in Michigan, where male-only lures were shown to attract more females than a male-female lure, which attracted a more equal proportion (Neri et al. 2018). Whether or not this is also true for fall migration is unknown. An alternate hypothesis is that standard field sexing methods are inaccurate. Beckett and Proudfoot (2012) found that most owls are correctly sexed comparing field sexing methods to more accurate genetic sexing, but that nearly 40% of saw-whets identified as unknown sex in the field were actually males. This could explain some of the skewed female to male capture ratio, but even without the designation of "unknown", there still are more females captured than males. Another hypothesis is that saw-whets have sex-specific migration strategies. This strategy is not uncommon in migratory birds and has been documented in the similar Boreal (Tengmalm's) Owl (Hipkiss 2002). Males and females may have differing dietary needs, not uncommon in birds of

prey because of their reversed sexual dimorphism (females are larger). These needs may only be satisfied if larger females migrate farther to places where food is more plentiful and the climate is milder. Males may benefit from staying farther north in winter so they are closer to the most prime breeding territories in spring. This strategy may explain why higher numbers of immature males are captured in irruption years. Immatures, with a lack of experience in hunting and finding premier territories, may not fare well farther north where winter food is less abundant and competition with more experienced adult males is higher (Beckett & Proudfoot 2011). Although females still dominate mist nets, males are captured in increasing numbers with increasing latitude, further supporting the idea that more males winter farther north. None of the hypotheses completely explain the skewed sex ratio.

Other milestones in banding of saw-whets were a chart based on wing length and weight for sexing birds as female, male, or unknown (Brinker 2000) and the demonstration that birds could be aged by the ultraviolet pattern of the underwing (Weidensaul et al. 2011). Saw-whets possess the pigment porphyrin that fluoresces as bright pink in a new feather and fades with time (pictured in Pruitt & Smith 2016). This allows easy determination of hatch-year birds (immatures) from after-hatch-year birds (adults). Additionally, saw-whets that are 1 year old can usually be distinguished from birds that are 2 years or older.

Since 1969, more than 298,000 saw-whets have been banded in North America. This is the result of considerable effort, largely in the north-central and northeastern U.S. and eastern Canada. In 1994, Project Owlnet (http://www.projectowlnet.org) was created by David Brinker and others to provide a network for banders working with saw-whets. As of autumn 2017, more than 150 banding stations were a part of this network (S. Huy pers. comm.). Researchers are concentrated in the northeastern states, the Upper Midwest, and Ontario, with scattered efforts along the Atlantic Coast and Appalachian Mountains to Georgia, and west to Alabama, Tennessee, Missouri, Arkansas, Oklahoma, Nebraska, Alberta, Saskatchewan, and southwestern British Columbia. There are fewer banding stations studying saw-whets west of the Mississippi River in the United States, with large data gaps in the Great Plains, Rocky Mountains, and along the West Coast. Knowledge of the species in the west is further muddied by altitudinal movements (Weidensaul 2015).

Perhaps one of the greatest questions remaining is: where do these migrants spend the winter? The answer is mostly unknown. Winter records exist for every state, including Texas, Florida, and Louisiana (Beyer 1900, Lesser & Stickly 1967, Miller & Loftin 1984). Two winter records even exist for Bermuda (data from Bird Banding Laboratory). The status of migratory individuals in winter in Mexico is not well understood, but there may be some overlap with resident saw-whets. Their winter range likely expands during irruption years and could explain isolated records mentioned above. Nevertheless, lack of research in the south makes it difficult to draw a line for the southern extent of their regular wintering range.

Historically, saw-whets have been associated with low, dense winter roosting sites in cedars, firs, or other short conifers less than five meters off the ground (Bent 1938). A few recent studies have shown this not to be universally true, demonstrating saw-whets seem to prefer whatever conifers are available for roosting. They appear to seek winter roost sites that will provide the most cover, usually coniferous trees, regardless of species or height above ground. In shorter Douglas-firs (*Pseudotsuga menziesii*) or cedars, roosts will be low because most available foliage is low. In taller red pines (*Pinus resinosa*), ponderosa pines (*P. ponderosa*), short-leaf pines (*P. echinata*), and their relatives, roosts are higher because that is where foliage is densest (Swengel & Swengel 1992, Fig. 7). Recent research shows saw-whets to be regular win-

Figure 7 - Typical tree shape, foliage density, and saw-whet roost locations in five tree species, from left to right: eastern red cedar (*Juniperus virginianus*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), and Norway spruce (*Picea abies*). Arrows indicate mean roost height and distance of roost from trunk (from Swengel & Swengel 1992).

Figura 7 - Forma típica da árvore, densidade da copa e localização dos poisos de mocho-amolador em cinco espécies de árvores, da esquerda para a direita: cedro-da-virgínia (*Juniperus virginianus*), pícea-branca (*Picea glauca*), pinheiro-cinzento (*Pinus banksiana*), pinheiro-silvestre (*Pinus resinosa*), e o abeto-falso (*Picea abies*). As setas indicam a altura média dos poisos e a distância destes ao tronco (adaptado de Swengel & Swengel 1992).

ter residents of open pine forest in northwestern Arkansas (M.L. Pruitt unpubl. data). This type of habitat is vast in the southern U.S. and could provide plenty of wintering habitat for saw-whets that seem to disappear after fall migration. Saw-whets have been located wintering in similar habitats in other places, where pines or other coniferous species dominate. Widespread records, irruptive tendencies, and a seeming ability to adapt to roosting in locally abundant species of conifer, seems to support the idea that saw-whet winter range may be dynamic.

A species that undergoes an autumn migration will naturally undergo some sort of return migration, but the saw-whet's spring migration is much less studied than autumn migration. A spring migration was first mentioned in the literature by Eaton (1914), who reported that saw-whets were often found by bird watchers in western New York in April and May. Further documentation of spring migration followed in the next several decades. Ornithologists suggested saw-whets were likely to be found in nearly any patch of forest along the southern shore of Lake Ontario in early April, especially following a warm front from the south (Barry 1952). It has been suggested that spring concentrations on the Great Lakes' southern shores are caused by birds waiting on suitable conditions to begin crossing the lake (Catling 1971). Today, stations in high-concentration areas are the most successful at capturing saw-whets during spring migration. One of the best examples is Whitefish Point Bird Observatory, located at the tip of Michigan's Upper Peninsula, likely also a result of pen-

insular effect. Conversely, some areas on the northern shores of the Great Lakes also see high concentrations, likely because migrants need rest and food after making the crossing.

A more comprehensive study was done by Catling (1971), conducted during a three-year period near Toronto. Saw-whets were found to begin their spring migration into the area in late-March, peaking in mid-April, and ending by late-April. Similarly, saw-whets on winter territories in the area no longer occupied that territory by late-March. Several saw-whets located during the study period clutched songbirds, suggesting migrant songbirds to be a food source during spring migration (Catling 1971). Banding data from 1955 to 1969 further supported this timing for southeastern Canada and the northern U.S, showing a peak in migration in late-March for New Jersey, mid-April for Ontario, and May for Michigan (Holroyd & Woods 1975).

Far fewer saw-whets are banded in spring compared to fall. Why this is can only be left to speculation, but there are several probable reasons. Foremost is the lack of effort to capture the species in spring. Considerably more effort is invested in capturing saw-whets in autumn. Secondly, saw-whets are seemingly less attracted to the audio lure used in fall. Additionally, the effect of periodicity in regional prey species, like *Microtus* and *Clethrionomys* has also been suggested as a reason for year-to-year variations in breeding saw-whets and, therefore, reduced capture rates during spring (Duncan et al. 2009).

A great deal has been learned about the Northern Saw-whet Owl in the last 100 years, before which very little was known about this secretive species. However, there is clearly much more to be learned about the saw-whet's breeding biology, winter distribution, and spring migration. Though widely captured during fall migration, even vast banding efforts provide little information in regard to movement ecology, specifically extent of migration, as recapture rates are low and few banding stations are located in the south. More comprehensive studies over a wider range will be required to fully understand the ecology of this species.

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