Science is driven by the generation of new ideas and hypotheses, but technological developments can also open new doors and, in some cases, play a significant role in advancing our understanding of the natural world. The development of the light-logging, archival ‘geolocator’, we argue, is one such technology that has tremendously advanced our knowledge of songbird migration and will also be important in helping us understand the causes of songbird declines.

Because of their small size (typically < 30g), songbirds have always presented a challenge for tracking long-distance migrations. Dating back over 100 years, attaching rings or bands to individuals has been the primary method for tracking bird movements (Bairlein and Becker 2011). However, not only are recapture rates of marked birds often <1% (USGS Bird Banding Laboratory 2016), but recovery of marked birds is restricted to a relatively small number of locations around the globe. Although the recent development of GPS-satellite tracking devices has provided the ability to remotely track year-round movements of a wide variety of animals with a high degree of precision (e.g., Bonfil et al. 2005, Alerstam et al. 2006, Mansfield et al. 2009), battery limitations have, thus far, prevented these devices from being light enough for most songbirds. The use of chemical markers, such as stable-isotopes, to estimate the geographic location of where tissue was grown in a previous period of the year has been revolutionary for linking the breeding and non-breeding sites of migratory birds (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Hobson 1999). Stable isotope analysis requires only a small
amount of tissue (typically < 1mg) and, unlike band recovery, individuals only have to be captured once. However, stable isotopes have notable limitations, including providing relatively low spatial resolution and the inability to track continuous movements throughout the year.

By the beginning of the 21st century there was, therefore, a pressing need to find a solution to track the year-round movements of songbirds, and this was when geolocators were first introduced. Light-logging geolocators are based on a simple concept ingeniously engineered into a small archival device (Figure 1). To estimate daily locations, they record just two pieces of information: light levels (solar irradiance) taken at regular intervals (usually every 2 or 10 min) throughout the day, and time (Afanasiev 2004). Longitude is estimated by the time of solar noon or midnight (calculated as the midway point between sunrise and sunset) and latitude is estimated by day length (calculated as the length of time between sunrise and sunset; Afanasiev 2004). Geolocators are ‘archival’ because data are stored on board the device. Remote download via satellite would require too much power and, therefore, increase size and weight. This means that geolocators must be retrieved the following year to acquire the data and determine an individual’s year-round migration. Depending on size, the devices can store approximately 8-12 months’ worth of daily location data.

Vsevolod Afanasiev and James Fox, engineers with the British Antarctic Survey (BAS), originally developed geolocators as leg attachments for tracking seabirds (e.g., Weimerskirch and Wilson 2000). In 2006, after discussions with Bridget Stutchbury, a professor at York University, they began to modify geolocators for songbirds. To fit small songbirds, the geolocator needed to be fit as a ‘backpack’ with a leg-loop harness (Figure 1a; Rappole and Tipton 1991) instead of attached to the leg, as was done in heavier seabirds. A small stalk also had to be designed so back feathers would not cover the light-sensing device (Figure 1b, Figure 2). Using a 1.2 g version of this newly-designed geolocator, Stutchbury and colleagues published the first study on songbirds that tracked the remarkable year-round migrations of both Wood Thrush (Hylocichla mustelina) and Purple Martin (Progne subis) from their breeding grounds in northern Pennsylvania to their tropical wintering grounds (Central and South America, respectively) and back (Stutchbury et al. 2009). They showed that geolocators could be used to identify migratory routes, the timing and rate of migration, key stopover sites during fall and spring migration, as well as overwintering sites at a level of spatial resolution never before seen.

The Stutchbury et al. (2009) proof-of-concept study opened the floodgates for new work on migratory songbirds in the following years, including a number of studies on species that breed in Ontario. For Grey Catbird (Dumetella carolinensis; Ryder et al. 2011), Swainson’s Thrush (Catharus ustulatus; Delmore et al. 2012), Purple Martin (Fraser et al. 2012), Ovenbird (Seiurus aurocapilla; Hallworth et al. 2015), and Barn Swallow (Hirundo rustica; Hobson et al. 2015), geolocators have been used to reveal that breeding populations in western North America
migrate to distinct, and often widely separated, wintering areas compared to populations in the east. Using geolocators, it has also been discovered that several species, such as Swainson’s Thrush (Delmore et al. 2012), Tree Swallows (Tachycineta bicolor; Bradley et al. 2014), and Barn Swallows (Hobson et al. 2015), cross the Gulf of Mexico during fall migration but migrate around the Gulf in the spring. This is likely due to wind patterns, where a tailwind assists the birds in a fall crossing, while less favourable wind conditions in the spring mean they must take a long detour (Bradley et al. 2014). Geolocators have also been used to demonstrate that male Savannah Sparrows (Passerculus sandwichensis) overwinter at higher latitudes in North America than females and that the further north a male overwinters the sooner he arrives on the breeding grounds to secure a territory (Woodworth et al. 2016). Many unusual and incredible migratory feats have also been uncovered using geolocators. Streby et al. (2015) used geolocators to show that Golden-winged Warblers (Vermivora chrysoptera) that had already reached their Tennessee breeding grounds travelled back south more than 1500 km to avoid dozens of tornadoes that swept through the region only to return after the storms had passed. In another study, DeLuca et al. (2015) used geolocators to provide the

Figure 2. A Blackpoll Warbler in Churchill, Manitoba fitted with a 0.5 g light-logging geolocator (model ML6440, Lotek Wireless) in spring 2016. The 9 mm white light stalk can be seen on the bird’s back. 
Photo: Christian Artuso
first direct evidence that the 12g Black-poll Warbler (*Setophaga striata*; Figure 2) flies over the Atlantic Ocean from the Maritimes to the Greater Antilles during fall migration, a distance of over 1500 km that takes up to three days to complete.

The use of geolocators in the last few years has uncovered many fascinating aspects of songbird migration but what is next? One exciting application is the use of these data to understand songbird population dynamics. With migratory animals, one of the greatest challenges is identifying which period in the annual cycle is driving population declines. Geolocators can be used to help address this problem because they provide unique data on migration routes, stopover sites and wintering areas. Using geolocators, we are now able to extract relevant climate or habitat information from all periods of the year. However, the challenge is even more complicated because individuals from a given breeding population may go to different non-breeding sites, potentially sharing sites with birds from other breeding populations. Migratory birds can, therefore, form complex networks in which breeding and non-breeding sites are linked through the mixing of individuals between seasons. Describing these migratory networks is of fundamental importance for understanding the causes of decline because events such as habitat loss that occur at one site may reverberate throughout the network (Sutherland and Dolman 1994, Taylor and Norris 2010). Geolocators will play a leading role in helping us describe these networks. For example, Stanley et al. (2015) used geolocators to describe the connections between multiple breeding and wintering populations of Wood Thrush and to then make recommendations about where conservation efforts would be most effectively focused for this species. Our current work using geolocators to describe the migratory network of Tree Swallows involves a collaboration of over 25 researchers across Canada and the U.S. We now have data from 137 geolocators deployed at 12 breeding sites ranging from Alaska to Nova Scotia, which will provide us with the most comprehensive description of a migratory network of any species to date.

The adoption of light-logging archival geolocators for songbirds has resulted in an incredible opportunity to track individual songbird movements throughout the annual cycle. However, like any method, there are drawbacks. Some, but not all, studies have shown that geolocators can result in reduced survival (Arlt et al. 2013, Gomez et al. 2014, Scandolara et al. 2014) and lower reproductive success (Arlt et al. 2013, Scandolara et al. 2014). Furthermore, because geolocators are archival, we can only obtain data from birds that have survived the entire annual cycle, which means that we gain no information from geolocators on the causes of mortality. New technologies, such as the recently established Motus automated radio telemetry array (see Mackenzie and Taylor article in this issue) and ICARUS (Wikelski et al. 2007), offer promise for tracking both movements and mortality, although their development is still in its infancy.
Regardless of what comes next, there is no doubt that light-logging geolocators have contributed enormously to our understanding of bird migration and will play a central role in helping us determine the causes of songbird declines.

Literature Cited


Samantha Knight and D. Ryan Norris
Department of Integrative Biology
University of Guelph
Guelph, Ontario N1G 2W1
E-mail: sknigh04@uoguelph.ca,