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Advances in tracking small migratory birds: a technical review of light-level geolocation

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ABSTRACT. Light-level geolocation data loggers, or geologgers, have recently been miniaturized to the extent that they can be deployed on small songbirds, allowing us to determine many previously unknown migration routes, breeding locations, and wintering sites. Use of geologgers on small birds has great potential to help address major research and conservation questions, but the method is not without its shortcomings. Among these shortcomings are the need to recapture birds after they have carried a device throughout a migration cycle and the potential for the devices to affect survival and behavior. We examined return rates of birds with geologgers in published and unpublished studies and found no evidence of a general negative effect of geologgers on survival, although there were a few individual studies where such an effect was evident. From these same studies, we found that most currently used harness materials are equivalent in terms of failure rates, and the most reliable geologgers are those made by the British Antarctic Survey (although these were also the largest geologgers used in the studies we examined). With regard to analysis methods, we believe there is much room for improvement. Use of online archiving of both data and analysis parameters would greatly improve the repeatability and transparency of geologger research.

RESUMEN. **Avances en el rastreo de pequeñas aves migratorias: una revisión técnica de geo-localizadores de niveles de luz**

Geo-localizadores de niveles de luz que registran datos, o geo-registradores, han sido recientemente miniaturizados para poder ser colocados en aves pequeñas, permitiéndonos comprobar muchos aspectos desconocidos como rutas migratorias, áreas de reproducción y lugares para pasar el invierno. El uso de los geo-registradores en aves pequeñas tienen un gran potencial para ayudar a responder grandes preguntas de investigación y conservación, pero el método no deja de tener sus defectos. Entre estos defectos están la necesidad de recapturar el ave después de que ha llevado este dispositivo a lo largo del ciclo de migración, y la capacidad que tiene este dispositivo para afectar la supervivencia y el comportamiento. Examinamos las tasas de retorno de aves con geo-registradores en artículos publicados y sin publicar, y no encontramos efectos negativos de los geo-registradores en la supervivencia, aunque hubo algunos estudios en donde dicho efecto fue evidente. Dentro de estos mismo estudios encontramos que los materiales de los arneses usados con mayor frecuencia tuvieron tasas de fracaso equivalentes, y los más seguros fueron los fabricados por British Antarctic Survey (aunque estos también fueron los de mayor tamaño en los estudios que examinamos). Respecto a los métodos de analíticos, creemos que hay mucho margen para mejorar. Utilizar recursos en línea para archivar los datos y parámetros analíticos mejorarían en gran medida la transparencia y la capacidad reproducir investigaciones realizadas con georegistradores.

Key words: animal tracking, data archive geolocator, Passeriformes, migratory songbirds

In 2007, Stutchbury et al. (2009) equipped 20 Purple Martins (*Progne subis*) and 14 Wood Thrushes (*Hylocichla mustelina*) with miniaturized archival geolocation tags (hereafter geologgers) supplied by the British Antarctic Survey (BAS, Cambridge, UK). They recovered seven of those geologgers the following spring, and each carried sufficient data to reveal a fascinating combination of rapid long-distance travel and prolonged stopover behavior by both species. Although geologgers had been in use for about two decades prior to this study (mostly used with marine vertebrates; Wilson et al. 1992, Welch and Eveson 1999, Phillips et al. 2004, Croxall et al. 2005), Stutchbury et al. (2009)

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were the first to employ this technique on a small terrestrial species. Since then, other investigators have used geologgers to generate a wealth of new information about songbird migration, including previously unknown wintering quarters (Beason et al. 2012), key stopover locations (Heckscher 2004), rates of migration (Tøttrup et al. 2012a, b), new interpretations of long-term banding data (Ryder et al. 2011), and connectivity maps of widespread populations (Stutchbury et al., unpubl. data). Numerous other projects are underway, including efforts to track birds as small as Hooded Warblers (*Setophaga citrine*, 9–11 g; Stutchbury, pers. comm.).

The principle behind geologger tracking is simple. Geologgers record light levels at regular time intervals. After a geologger has been attached to a bird for a desired time period, its stored data can be used to infer solar positions (i.e., the relationship between the sun and the horizon) that, in turn, can be used to estimate the location of the geologger on the earth (Hill and Braun 2001, Ekstrom 2004). Of course, this tracking method is far from perfect. First, birds must not only be captured to deploy geologgers, they must be recaptured to recover the data. As a result, it may be necessary to tag three or four birds for every geologger recovered. Also, because of error associated with unknown degrees of shading of the geologger, a bird's exact location cannot be determined using geologgers. At best, error estimates are large compared to satellite-based tracking, particularly for latitude, with documented errors on the order of 200 km or more (Fudickar et al. 2012, Lisovski et al. 2012). Nevertheless, geologgers have proven to be a powerful tool for resolving basic questions about migration routes and the timing of migratory movements (Bridge et al. 2011). Moreover, given that the mass of satellite and GPS tags usually exceeds 5 g, geologgers are currently the only tracking devices suitable for use on small birds (<100 g) that provide location data on a continental scale.

Although most ornithologists likely know about geologgers and dozens of geologger-based studies are currently underway, the methodology behind use of these devices is far from standardized, especially with regard to small terrestrial migrants. Therefore, our objectives in this review are to (1) summarize current practices regarding use of geologgers and analysis of light-level data, (2) critically evaluate these practices to help derive much-needed standards for geologger studies, and (3) evaluate future prospects for geologger-based research. We restrict our scope to studies of small songbirds because the constraints and difficulties associated with studying terrestrial birds (i.e., species that may occupy shaded microhabitats) and using small (<2 g) geologgers are distinct from those of earlier studies with larger species in open (marine) habitats. We hope to catalyze a dialog regarding the use of geologgers in studies of small migratory birds and how best to manage the data in terms of analysis, presentation, and dissemination.

GEOLOGGERS: CURRENT DESIGNS AND AVAILABILITY

The specific designs and components of currently available geologgers are proprietary information so we cannot provide details sufficient to copy an existing device. However, the basic framework of available sub-gram geologgers resembles the design published by Afanasyev et al. (2004) where a sensor, a clock, and a memory device are integrated via a microprocessor. As more sophisticated microprocessors have become available, some geologgers may use clocks or memory built into the microprocessor, but the same four elements are common to all geologgers.

Geologgers must have sufficient battery power to maintain an accurate clock (i.e., a crystal oscillator and counting mechanism) for as long as data are to be collected. Sensor readings and data logging happen in a fraction of a second and occur only periodically during deployment. Between these events, the microprocessor can enter a low-power sleep mode. However, the clock runs at all times and is a constant drain on the battery. Therefore, battery requirements are the primary limitation on miniaturizing geologgers. Most clocks and microprocessors function over a limited voltage range, generally 2–5 V. This makes it difficult to find an appropriate power source, especially because batteries small enough for tiny geologgers (i.e., batteries that weigh well under 0.5 g) are not widely available. More specifically, available battery options include silver oxide watch batteries (rated at 1.5 V) and rechargeable lithium batteries that are nominally 3–3.3 V. These constraints have spurred several

Table 1. Comparison of return rates of small terrestrial migratory birds with leg bands and geologgers. Each row corresponds to a particular species, population, or deployment of devices, and studies are sorted by the body mass of focal species (smallest first). The tag type column indicates the maker of the tag and, when applicable, the length of the light stalk in parentheses. Returns are indicated as ratios of the number of birds returned (re-sighted or recaptured) to the number tagged or banded, with percentages shown in parentheses. "Returns, bands only" lists return rates of conspecifics without geologgers that are comparable to return rates of birds with geologgers. These data were not available for some studies, and instances in which comparisons are compromised or questionable are explained with footnotes to the "Returns, bands only" column. Bold print in the "Returns, geologgers" column indicates where return rates for birds with geologgers was >10% lower than for birds with leg bands only.

Species	Body mass (g)	Years	Location	Tag type	Tag weight (g)	Returns, geologgers	Returns, bands only	Source
Pied Flycatcher (*Ficedula hypoleuca*)	12	2010–2012	Netherlands	OU-Cornell	0.6	17/59 (29%)	37/135 (27%)	C. Both and J. Ouwehand (unpubl.)
Aquatic Warbler (*Acrocephalus paludicola*)	12	2010–2011	Ukraine	SOI-GDL2	0.6–0.67	6/30 (20%)	6/16 (38%)	Salewski et al. 2013
Painted Bunting (*Passerina ciris*)	15	2010–2012	Oklahoma	OU-Cornell	0.6–0.7	45/200 (23%)	15/97 (15%)	Contina et al. in press
Tree Swallow (*Tachycineta bicolor*)	20	2011–2012	New York, Wisconsin	OU-Cornell	0.7–0.8	19/71 (27%)	–	A. Laughlin, L. Whittingham, P. Dunn, and C. Taylor (unpubl.)
Red-eyed Vireo (*Vireo olivaceus*)	20	2011–2012	Pennsylvania	BAS MK20S (5 mm)	0.7	10/26 (39%)	5/11 (45%)	Callo et al. (in press)
Northern Wheatear (*Oenanthe oenanthe*)	23	2009–2010	Germany	BAS Mk10S (13 mm)	1.4	9/20 (45%)	58/107 (54%)	Schmaljohann et al. 2012
Northern Wheatear	25	2010–2011	Alaska	BAS Mk10S (13 mm)	1.4	5/30 (16%)	N/A	Bairlein et al. 2012

Continued

Table 1. Continued.

Species	Body mass (g)	Years	Location	Tag type	Tag weight (g)	Returns, geologgers	Returns, bands only	Source
Northern Wheatear	26	2010–2012	Mongolia	OU-Cornell	0.7–0.8	12/60 (20%)	N/A	N. Batbayar and E. Bridge (unpubl.)
Thrush Nightingale (*Luscinia luscinia*)	26	2009–2012	Scandinavia	BAS Mk10S (8 mm)	0.9	10/44 (23%)	37/167 (22%)[a]	Sorjonen 1987, Stach et al. 2012, Tøttrup et al. 2012a
Lark Sparrow (*Chondestes grammacus*)	26	2011–2012	Ohio	OU-Cornell	0.7–0.8	9/21 (43%)	50/81 (62%)[b]	J. Ross, E. Bridge, M. Rozmarynowycz, and V. Bingman (unpubl.)
Bicknell's Thrush (*Catharus bicknelli*)	27	2009–2010	USA – 3 sites	BAS Mk10 (15 mm)	1.2	4/45 (9%)	–	Renfrew et al. in press
Bicknell's Thrush	27	2010–2011	USA – 3 sites	BAS Mk12 (15 mm)	0.9	13/60 (22%)	–	Renfrew et al. in press
Northern Wheatear (*Oenanthe oenanthe*)	28	2010–2011	Nunavut	BAS Mk10S (13 mm)	1.4	2/16 (13%)	2/33 (6%)	Bairlein et al. 2012
Red-backed Shrike (*Lanius collurio*)	30	2009–2012	Scandinavia	BAS Mk10S (8 mm)	1.1	26/151 (17%)	(~24% – 37%)[a]	Šimek 2001, Pasinelli et al. 2007, Tøttrup et al. 2011
Swainson's Thrush (*Catharus ustulatus*)	31	2010–2011	British Columbia	BAS MK12S (15 mm)	1.1–1.2	10/39 (26%)	(~36%)[a]	Evans et al. 1998, Delmore et al. 2012
Fork-tailed Flycatcher (*Tyrannus savana*)	31	2009–2010	Argentina	BAS MK12S and BAS Mk10S (15 mm)	0.9–1.2	9/44 (20%)	N/A	A. Jahn, V. Cueto, D. Tuero, D. Levey, and D. Masson (unpubl.)

Continued

Table 1. Continued.

Species	Body mass (g)	Years	Location	Tag type	Tag weight (g)	Returns, geologgers	Returns, bands only	Source
Fork-tailed Flycatcher	32	2010–2011	Bolivia	BAS Mk10S (15 mm)	1.2	0/15 (0%)	N/A	A. Jahn, D. Levey, and A. Mamani, (unpubl.)
Golden-crowned Sparrow (*Zonotrichia atricapilla*)	33	2010[c]	California	BAS Mk10S (15 mm)	1.1	11/33 (33%)[d]	11/28 (39%)	Seavy et al. 2012
Veery (*Catharus fuscescens*)	35	2009–2010	Delaware	BAS Mk14S (20 mm)	1.5	16/24 (67%)[e]	(62%)[g]	Heckscher et al. 2011
Snow Bunting (*Plectrophenax nivalis*)	35	2009–2011	Nunavut	BAS MK12S and BAS MK20AS	1.1g	13/90 (14%)	N/A	Macdonald et al. 2012
Gray Catbird (*Dumetella carolinensis*)	36	2009–2010	Maryland	BAS Mk10S (15 mm)	1.6	7/22 (32%)	88/294 (30%)	Ryder et al. 2011
Scissor-tailed Flycatcher (*Tyrannus forficatus*)	36	2011–2012	Oklahoma	BAS Mk20ASLT (15 mm)	0.9	5/38 (13%)	1/3 (33%)[g]	A. Jahn, M. Husak, D. Landoll, and J. Fox, (unpubl.)
Eastern Kingbird (*Tyrannus tyrannus*)	37	2011–2012	Oklahoma	BAS Mk20ASLT (15 mm)	0.9	1/2 (50%)	N/A	A. Jahn, M. Husak, D. Landoll, and J. Fox, (unpubl.)
Tropical Kingbird (*Tyrannus melancholicus*)	43	2010–2011	Argentina	BAS MK12S and BAS Mk10S (15 mm)	0.9–1.2	1/5 (20%)	1/1 (100%)[g]	A. Jahn, V. Cueto, D. Tuero, D. Levey, and D. Masson (unpubl.)
White-throated Kingbird (*Tyrannus albogularis*)	40	2010–2011	Bolivia	BAS Mk10S (15 mm)	1.2	2/8 (25%)	1/5 (20%)	A. Jahn, D. Levey, O. Barroso, and A. Mamani, (unpubl.)

Continued

Table 1. Continued.

Species	Body mass (g)	Years	Location	Tag type	Tag weight (g)	Returns, geologgers	Returns, bands only	Source
Western Kingbird (*Tyrannus verticalis*)	40	2011–2012	Oklahoma	BAS Mk20ASLT (15 mm)	0.9	16/40 (40%)	3/9 (33%)	A. Jahn, M. Husak, D. Landoll, and J. Fox, (unpub.)
Common Swift	43	2009–2010	Sweden	BAS Mk10	1.3	6/8 (75%)	(~80%)[a]	Perrins 1971, Akesson et al. 2012
Purple Martin (*Progne subis*)	45	2011–2012	Oklahoma	OU-Cornell	0.75	3/6 (50%)	N/A	E. Bridge and J. Kelly (unpubl.)
Purple Martin	49	2007–2008	Pennsylvania	BAS Mk14S (20 mm)	1.5	2/18 (11%)	137/330 (41%)	Stutchbury et al. 2009
Purple Martin	49	2008–2009	Pennsylvania	BAS Mk10S (15 mm)	1.1	3/16 (19%)	93/255 (36%)	Stutchbury, unpubl.
Purple Martin	49	2009–2012	Pennsylvania	BAS Mk10S (5–10 mm)	1.1	39/87 (45%)	104/341 (35%)	K. Fraser and B. Stutchbury, unpubl.
Wood Thrush (*Hylocichla mustelina*)	50	2007–2010	Pennsylvania	BAS Mk14S (20 mm)	1.5	37/97 (38%)	29/111 (26%)	Stutchbury et al. 2009; C. Stanley, E. McKinnon, K. Fraser, M. MacPherson, and B. Stutchbury (unpubl.)
Wood Thrush	50	2008–2010	Costa Rica	BAS Mk14S (20 mm)	1.5	25/109 (23%)	7/100 (7%)	C. Stanley, E. McKinnon, K. Fraser, M. MacPherson, and B. Stutchbury (unpubl.)
Wood Thrush	50	2008–2010	Belize	BAS Mk14S (20 mm)	1.5	10/73 (14%)	9/78 (12%)	C. Stanley, E. McKinnon, K. Fraser, M. MacPherson, and B. Stutchbury (unpubl.)
Northern Black Swift (*Cypseloides niger borealis*)	51	2010–2011	Colorado	BAS Mk10S (10 mm)	1.2	3/4 (75%)	(41%)[f]	Beason et al. 2012

Continued

Table 1. Continued.

Species	Body mass (g)	Years	Location	Tag type	Tag weight (g)	Returns, geologgers	Returns, bands only	Source
European Bee-eater (*Merops apiaster*)	54	2010–2011	Germany	SOI-GDL1.0	1	5/40 (13%)	20/40 (50%)	Arbeiter et al. 2012
Rusty Blackbird (*Euphagus carolinus*)	55	2009–2010	Alaska	BAS Mk10B-S (10 mm)	2	3/17 (18%)	(60%)[b]	Johnson et al. 2012
Yellow-billed Cuckoo (*Coccyzus americanus*)	60	2009–2010	New Mexico	BAS Mk14S (20 mm)	1.5	1/13 (8%)	5/52 (10%)[a]	Halterman 2009, Sechrist et al. 2012
Hoopoe (*Upupa epops*)	70	2008–2009	Switzerland	BAS Mk14S (20 mm)	1.8	5/19 (26%)	25/111 (23%)	Bächler et al. 2010
American Robin (*Turdus migratorius*)	80	2009–2011	Kentucky	BAS Mk14S (20 mm)	1.8	10/37 (27%)	3/11 (27%)	D. Brown (unpubl.)

[a]From a previous and separate study.
[b]From previous year or years.
[c]Recaptured on wintering grounds during same year as deployment.
[d]Seven of the returned birds lost their tags.
[e]Nine of the returned birds lost their tags.
[f]Multi-year average.
[g]Sample too small for valid comparison.

innovations with regard to geologger design (see below).

Another concern is that the light sensor must be positioned so it is not covered by feathers. Although elevating the sensor seems simple enough, doing so adds weight and makes geologgers vulnerable to mechanical damage, especially because some birds may tug at them until they become habituated or possibly for the entire deployment. Some geologgers, such as those leg-mounted on shorebirds (e.g., Burger et al. 2012), do not elevate the sensor, but these are rarely used on small landbirds (Table 1) because a stalk is usually needed for backpack mounts (but see Akesson et al. 2012). Thus, stalkless designs are not considered in our review.

The BAS geologgers used by Stutchbury et al. (2009) and several others are the most commonly used (Table 1). They typically employ two 1.5-V silver oxide batteries in series to generate ~3 V. The light sensor is elevated by means of a thin, flexible stalk that extends both dorsally and ventrally from the bird's back (Fig. 1A). BAS has been making geologgers for about a decade, but only more recent models are small enough for passerines; the smallest currently available weighs 0.6 g without harness material. BAS geologgers are made and distributed by both the BAS and Biotrack LTD (Wareham, Dorset, UK; partnered with Lotek Wireless Inc., Newmarket, Ontario, Canada). The weight of geologgers with harness material ranges from 0.7 to 1.8 g depending on the model and length of the stalk.

The Swiss Ornithological Institute (SOI) has developed a geologger with a single 1.5-V cell to reduce size and weight. To do this, the geologger incorporates a DC-DC boost regulator to increase the voltage from the battery. This same design feature allows batteries to be drained to a very low level before the device ceases to function. Another innovation by the SOI is that, instead of elevating the sensor, SOI geologgers have the sensor attached directly to the circuit board with a small section of fiber-optic material extending upward from the sensor and above the bird's feathers (Fig. 1B). This innovation maintains a two-dimensional layout to the circuit board, which simplifies assembly, and the fiber-optic stalk can be customized to fit an individual bird by simply clipping it at the appropriate height. Weight of the geologger

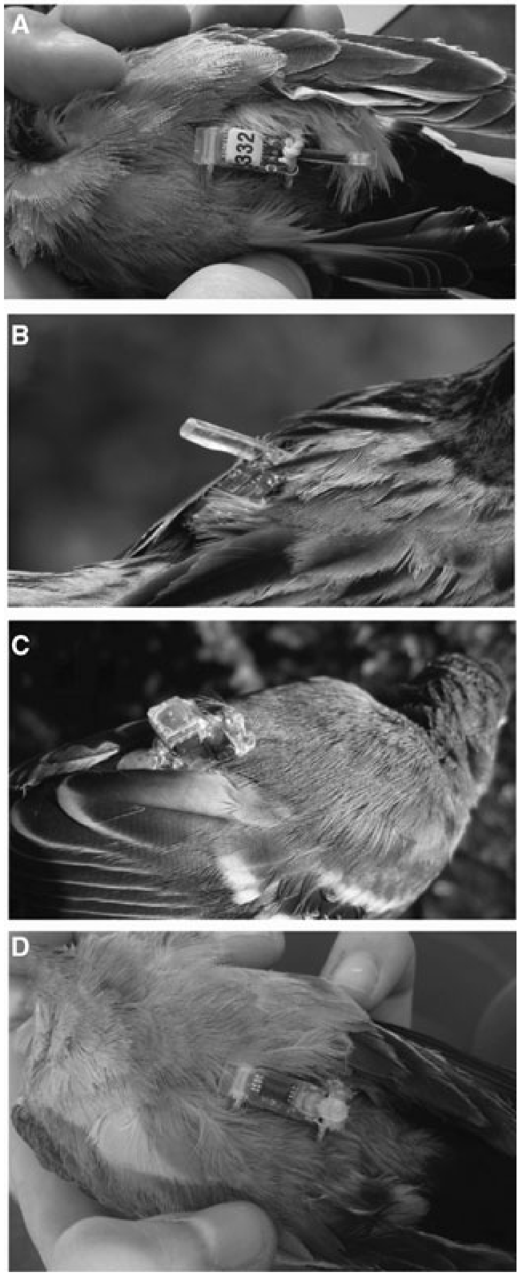

Fig. 1. Geologgers commonly in use in studies of small songbirds: (A) BAS Mk10S with a 15-mm stalk for the light sensor (photo by Alex Jahn), (B) GL05AE10 from the SOI with a fiber-optic stem that conducts light from above the feathers to the light sensor (photo by Volker Salewski), (C) I-beam shaped, OU-Cornell geologger with a solar cell, and (D) Migrate Tech geologger (photo by Alex Jahn).

(with harness material) is approximately 0.5 g (F. Liechti, pers. comm.).

A collaborative effort by researchers at the University of Oklahoma and Cornell University has resulted in a geologger that uses a small solar cell to opportunistically charge a 3-V lithium battery (Fig. 1C). The solar cell also acts as a light sensor, minimizing the number of parts needed. This design has the advantage of being simple and inexpensive (less optimization needed because solar power is abundant), but use of this design has proved problematic with birds that remain in shaded habitats for extended periods of time. In such cases, the battery can become drained to the point where the clock stops, data collection ceases, and subsequent recovery of logging operations is not possible. The solar cell is elevated above the feathers by means of a flexible circuit board folded into an I-beam shape, with the solar cell positioned at the top of the apparatus. The use of a flexible circuit board (FCB) presents some manufacturing challenges, and sharp folds in the board that intersect copper traces in the FCB design have caused geologger failure. These geologgers ranged in weight from 0.55 g to 0.8 g (including harness), depending on battery size. They are currently being tested by a small group of collaborators, and devices and designs will likely be made publically available in 2014.

The most recent producer of geologgers is Migrate Technology Ltd (Cambridge, UK). Migrate Technology geologgers variously combine features present on other devices, like the dual battery arrangement in the BAS geologgers and the fiber optic stalk in the SOI geologgers (Fig. 1D). Migrate Technology geologgers also offer full-range light sensing (most other geologgers are sensitive only to low light levels), temperature logging, and conductivity indices that indicate whether the geologger is wet. Migrate Technology geologgers weigh as little as 0.55 g, with experimental devices weighing 0.5 g, excluding harness materials.

GEOLOGGER SUCCESS AND LOSS RATES

Based on published and unpublished reports, we compiled data concerning geologger success rates. In evaluating success rates, we classified a geologger as a total failure if it provided no useful migration data (i.e., stopped working before the bird initiated a migratory flight), and as a partial failure if it provided useful data about either spring or fall migration, but not the full migration cycle. We urge caution in interpreting these results because success rates vary considerably among studies, and new designs are frequently introduced that may improve success rates.

BAS geologgers appear to have the best record of success. For studies where information was provided (Table 1), 126 BAS geologgers were recovered, with 13 (10%) total failures and 15 (12%) partial failures. Fraser et al. (2012) compiled several years of tracking data for Purple Martins (some of which overlaps with the data in Table 1) and reported a somewhat lower success rate for BAS geologgers, with full migration route data for 95 of 120 geologgers recovered (79.2%).

Few data are available for SOI geologgers. Arbeiter et al. (2012) and Salewski et al. (2013) report a combined total of eight SOI geologgers recovered (3 were lost from returning birds). Of the recovered geologgers, one failed completely and six failed to provide a full data set. The OU-Cornell geologger is clearly the worst with regard to successful data collection. Of 91 recoveries of the most recent design, there were 42 total failures (46%) and 30 partial failures (33%). However, the SOI and OU-Cornell geologgers were considerably smaller than the BAS geologgers, and increased failure rates should be expected with smaller geologgers. Batteries for geologgers weighing well under 1 g provide just enough power to maintain functionality, increasing the likelihood of failure due to such things as exposure to moisture or low temperatures. Geologgers made by Migration Technology have yet to undergo year-long tests in the field by independent researchers so we cannot yet comment on their reliability.

Loss of geologgers has been reported in some studies. For example, Seavy et al. (2012) reported the loss of geologgers from seven of 11 birds that returned following a migration cycle, and Heckscher et al. (2011) reported that nine of 16 returning birds lost geologgers. Most investigators have used leg-loop harnesses to attach geologgers (Rappole and Tipton 1991), but some investigators have used other types of harnesses, such as backpacks anchored around the wings (see Beason et al. 2012). Commonly used harness materials include Teflon ribbon, Kevlar thread, silicone monofilament, and beading thread. Evaluating the efficacy of different harnesses and harness materials across studies is difficult because the skills of researchers in making and attaching harnesses may vary and the behavior of different species may have a greater effect on loss of geologgers, if not more so, than the type of harness and materials used. Nevertheless, we attempted to compile all available information about loss of geologgers from both published and unpublished studies.

Four of 13 geologgers (31%) were lost in studies where a silicone–rubber material (MVQ Arcus, Germany) was used as harness material (Bairlein et al. 2012, Salewski et al. 2013), suggesting that this material should probably not be used. Otherwise, there is no clear choice with regard to harness material. Seavey et al. (2012) and Heckscher et al. (2011) reported considerable loss of geologgers (7 of 11 birds) using Kevlar thread and Teflon ribbon (9 of 16 birds), respectively. In contrast, other investigators using Kevlar thread have reported only two geologgers lost from 38 returning birds (5.3%, unpublished data from Jahn et al. in Table 1), and no losses out of 26 returns with Teflon ribbon (Ryder et al. 2011, Macdonald et al. 2012, Beason et al. 2012, Johnson et al. 2012). Fraser et al. (2012) reported harness failures for 10% of 120 returning Purple Martins when using polypropylene thread as harness material, and only 3% failures with Teflon ribbon. For many of the OU-Cornell tags, we have used transparent, monofilament, elastic beading thread (a combination of polyethylene and polyester called Stretch Magic™; Pepperell Braiding Company, Pepperell, MA), and only two of 64 returning birds (3%) lost their geologgers (unpubl. data). We have observed that individuals in some species, for example, Painted Buntings (*Passerina ciris*) and Northern Wheatears (*Oenanthe oenanthe*), spend considerable time picking at backpack mounts with their beaks. For such species, a robust monofilament may be preferable to a stranded or woven material because the birds may eventually sever these materials strand by strand.

EFFECTS OF GEOLOGGERS ON BIRDS

Authors of almost every published geologger study cite a 5% or 3% body mass rule of thumb in their methods to justify the assumption that the effect of geologgers on survival and behavior is minimal. However, the source of this rule and the reasoning behind it are unclear (Barron et al. 2010). Moreover, in addition to weight, investigators should also consider the aerodynamic burden imposed by geologgers. Based on wind-tunnel measurements of a preserved bird torso, Bowlin et al. (2010) measured drag associated with BAS and SOI geologgers and found that, when incorporated into an avian flight model, the effects of drag caused a slightly greater decrease in predicted flight range than an increase in weight of 1 g. The combined effects of geologger weight and drag led to predicted decreases in flight range of <5% in larger birds (Red Knot, *Calidris canutus*, 129 g) to almost 20% in small species (Eurasian Siskin, *Carduelis spinus*, 10 g; Bowlin et al. 2010).

Although considerable data are available concerning the effects of radio-transmitters on birds (Barron et al. 2010), the elevated sensor, mounting style, and long-term deployment of geologgers limits the inference from studies of other devices. Possible effects of geologgers on small birds are also a concern for permitting agencies because, at present, there have been too few pilot studies to draw any conclusions. To help address these concerns, we compiled return rate-data from 38 published and unpublished studies of species ranging in size from 12 to 80 g (Table 1). Of these studies, return rates for both birds with geologgers and birds that were only banded were reported in 24. Decreased return rates for birds with geologgers were reported in nine of these studies (38%), and decreases of more than 10% were reported in five studies (21%). Decreased return rates were generally reported for species weighing $\leq$ 35 g. Among larger birds, substantial decreases in return rates were reported only for European Bee-eaters (*Merops apiaster*; Arbeiter et al. 2012) and Purple Martins (Stutchbury et al. 2009). However, for Purple Martins, subsequent use of a different tag design with a shorter stalk seemed to eliminate geologger-related mortality (B. Stutchbury, unpubl. data).

Although the effects of geologgers on return rates appear to be minimal in most studies (Table 1), we urge caution in evaluating these findings. We did not attempt a true meta-analysis because comparisons among studies are confounded by methodological differences. Moreover, there may be biases in the selection of birds equipped with geologgers and the effort expended in recapturing them. Researchers may select larger or more robust individuals for geologger deployments, or birds with geologgers may be more readily sighted in the field than birds with only leg bands. Investigators wanting to predict the possible effects of geologgers on a particular species should examine results reported for similar species rather than the general trends across all species. Foraging mode, body size, and numerous other factors likely influence the ability of different species to cope with the added mass and aerodynamic burden of geologgers.

Return rates of birds fitted with geologgers have generally been relatively high in most studies to date (Table 1), but additional negative effects may emerge as researchers attempt geologger studies with smaller species. Moreover, effects on life history parameters other than survival may also become apparent as investigators focus more on phenology, behavior, and breeding success, all of which may be impacted by geologgers. We urge investigators who use geologgers to do so in conjunction with typical banding studies so we can continue to compare birds with geologgers to others in the population and improve our understanding of how geologgers affect behavior and survival.

ANALYSIS OF LIGHT-LEVEL DATA

In most geologger studies, light-level data are translated into coordinates using a suite of software tools referred to as BAStrack, which is owned and distributed by the British Antarctic Survey. Analyses performed with BAStrack first establish a correspondence between a somewhat arbitrary light level (usually a relatively low value) and a particular sun angle based on several days of data when the geologger was at a known geographic location (and preferably attached to the bird to be tracked). Based on this calibration procedure, the program generates estimates of twilight times, and these twilight times are used to generate two locations per day–one corresponding to noon and one to midnight—based on the length of the day/night and the time of solar noon/midnight (Hill 1994). A functionally similar analysis system is sold by Jenson Software (Multitrace, www.jensen-software.com), and there also is a free R package called GeoLight that can perform threshold-based geologger analyses (Lisovski and Hahn 2012).

The thresholding method executed by these software tools is simple and broadly applicable, and results can be generated and visualized quickly. However, there are a few drawbacks to the method that may compromise some studies, depending on the quality of the data and the questions to be addressed. One concern is that the thresholding method provides little insight into the amount of error associated with location data; the output consists of a simple list of coordinates. Some investigators address error by extrapolating from other studies (e.g., mock deployments or "rooftop data"; see Fudickar et al. 2011, Lisovski et al. 2012) or data from the calibration period. This practice may provide a general idea of the scope of potential error, but does not address the possibility of changes in error throughout the course of the deployment that could be caused, for example, by a change in a bird's local habitat between breeding and wintering areas.

Another common and potentially problematic practice is to visually inspect geologger data, either the light time-series profile or location data, and flag or remove data that appear to be outliers. BAS software allows users to assign confidence scores to each threshold transition wherein they rate the quality of the light profile on a scale from 0 (poor) to 9 (good). Later, when viewing a migration track, investigators can then choose to flag or remove those locations that correspond to low quality light profiles.

Although it may be clear to someone viewing a data set that some locations or twilight events are too noisy to be informative, the subjective elimination of data violates the scientific principle of repeatability. Judging the quality of locations or light profiles by visual inspection is a subjective exercise, and the outcome of such an analysis will likely differ from person to person. For most studies published to date, the basic research questions underlying the study do not hinge on a small number of apparently flawed data points, and subjective elimination does not negate the value of the study. However, there are some clearly problematic examples. For example, MacDonald et al. (2012) visually determined confidence scores that were used to weight data points used in a kernel density estimate. This weighting could have profound effects on the size of the kernel density estimates, and repeatability of the analysis is limited without the original confidence scores.

When eliminating data from a migration route, we suggest that investigators describe the criteria for rating transitions or deleting outliers and provide examples of high-, medium-, and low-quality light profiles so readers better understand the underlying evaluation of light-level data. Researchers should also indicate the number of locations eliminated due to apparent shading error and the number of points deemed acceptable. Geolight incorporates a distance filter that allows users to remove location estimates that are isolated from the others (Lisovski and Hahn 2012). By reporting the parameters of the distance filter, investigators can potentially eliminate obvious outliers and the analysis would be repeatable.

Another problem is that the thresholding process cannot ascribe latitudes to light data near the time of the equinoxes, when day length is effectively the same for all locations the world over. Most authors have dealt with this by eliminating from consideration all latitudes within *x* number of days of each equinox. The omission window is sometimes determined *a priori*, or may be determined after visual inspection of the data. We regard either option as acceptable as long as the omission window is clearly defined.

An alternative to the thresholding method for generating locations is template fitting. Template fitting involves generating an astrological model that simulates light-level data as a function of time and position and then fitting this model to observed geologger data to derive the most likely set of geographical locations. Template fitting is more complex and difficult to implement than thresholding, and has not been widely applied in geologger studies. A few investigators (i.e., Seavy et al. 2012, Contina et al., in press) have used a simplified form of template fitting implemented in the R package tripEstimaton (Sumner et al. 2009) to analyze geologger data). This method involves fitting curves to twilight periods, but does not apply a template to the entire data set. To our knowledge, true template fitting has not yet been applied to studies of small songbirds. Therefore, we discuss it further in the next section about future directions.

In addition to implementing curve-fitting functions, the tripEstimation package allows for the application of an animal movement model to enhance the overall estimate of a migration route. Movement models typically apply a user-defined distribution of daily movement rates to constrain the raw location data (Schick et al. 2008). In tripEstimation, the movement model is combined with location data (or light-level data) and other relevant environmental data (e.g., sea surface mask for terrestrial species) within a Bayesian framework, and the package uses Markov Chain Monte Carlo methods to approximate the posterior distribution of locations for a given migration route (Sumner et al. 2009).

An example of a data set analyzed using both simple thresholding and using a movement model implemented in tripEstimation is provided in Figure 2. This example illustrates that analysis methods employing movement models offer a way to limit the influence of occasional low-quality light data, and can be used to infer an estimate of location during the equinox periods. The output of a movement model is dependent on several assumptions about how and when animals move, but, if these assumptions are presented along with other model parameters, any analysis should be repeatable.

The choice of an analysis method depends upon the goals of a study. If the goal is to construct the most realistic migration route possible, then use of a movement model may be warranted. If a crude evaluation of wintering quarters or stopover sites is needed, then simple thresholding may be adequate. If questions relate to the timing of large-scale movements, then it may be best to forego the generation of location data and examine shifts in light patterns or twilight times. We note that GeoLight allows for a "changepoint" analysis of this sort (Lisovski and Hahn 2012).

FUTURE DIRECTIONS

Improved devices. Tracking technology has benefitted from rapid technological advances and increasing miniaturization of complex electronics. As a result, Wikelski et al. (2012) suggested that geologgers would soon be supplanted by a miniaturized satellite transmitter. However, tracking devices based on long-distance signal transmission face a fundamental limit in their design. Signal transmission requires energy that must come from a battery of sufficient capacity. Because of this fundamental constraint, transmission-based transmitters small enough for songbirds that function on a continental

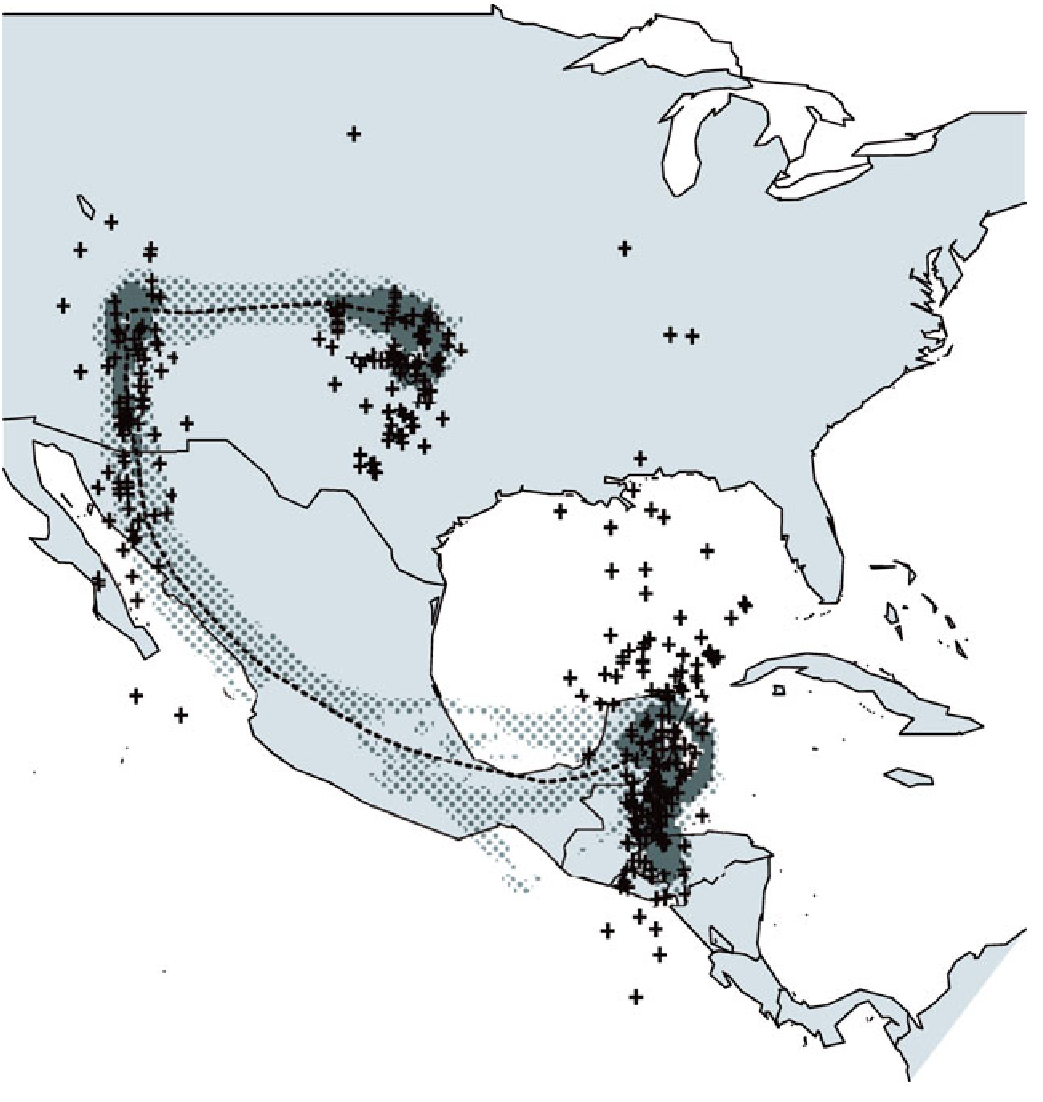

Fig. 2. Example of geologger data interpreted with simple thresholding in GeoLight (crosses) and a migration path derived from curve fitting and an animal movement model in tripEstimation (gray shading and stippling). Shaded regions represent likely stationary areas and stippled areas correspond to migration. The dotted line shows the most likely path taken by a migrating Painted Bunting based on the posterior probability distribution. For a full description of these analyses, see Contina et al. (in press).

scale seem unlikely unless there is an unforeseen breakthrough in battery technology (Bridge et al. 2011). The ICARUS project (International Cooperative for Animal Research Using Space; see Wikelski and Rienks 2008) will likely allow for global tracking of some small animals via a sophisticated space-based receiver system that can detect faint radio signals from transmitters significantly smaller than current satellite tracking devices. However, the possibility of a 0.5-g ICARUS tag (small enough for most songbirds) that can deliver a sufficient signal for an entire migration cycle has not yet been demonstrated (Pennisi 2011).

Minimum energy requirements (and battery size) for data-logging devices are not so clearly defined because more efficient components for collecting and storing sensor data are constantly emerging. As a result, we may soon see geologgers that can operate with extremely small batteries. Chen et al. (2010) demonstrated the potential for stand-alone data logging sensor systems in a 3.5 × 2.5-mm module that can run for several years on a 12-μAh, 2.9-mm^2, film-based battery charged by four 1-mm^2 solar cells. Sub-gram geologgers may also be capable of short-range wireless data transfers. There are currently wireless solar-powered sensor systems with a total volume of 1.5 mm^3 that are small enough to be used as eye implants (Chen et al. 2011). Applying similar technologies to geologgers would mean that data could be recovered by bringing a transceiver near a tagged bird rather than having to capture it. In light of these existing technologies, we may soon see geologgers so small that the primary concern about weight will relate to the harness material rather than the geologger itself.

Improved software and archiving. There is great potential to improve the analysis tools available for geologger data. Thresholding techniques currently used by most researchers fail to exploit all the data that can potentially inform geologger location estimates. For example, thresholding tools cannot derive latitudinal values during the spring and fall equinox periods because day length is effectively uniform across the globe. However, latitudinal differences in the rate of sunrise and sunset exist throughout the year (i.e., the rate of change of sun elevation). At the equator, the sun appears to ascend and descend at an angle perpendicular to the horizon and, at solar noon, the sun is directly overhead during an equinox. At more northern or southern latitudes, the sun traverses the sky at an angle $<90^\circ$ relative to the horizon, and the sun is not directly overhead at its apex. By using geologgers capable of recording light levels across the range of outdoor light variation and by employing template-fitting methods, deriving rough latitudinal estimates from the rate of light-level change associated with sun elevation should be possible.

Template-fitting techniques also offer an objective means of quantifying the quality of light data by numerically evaluating how well a given light profile corresponds to the expected profile. Expected profiles would consist of empirically derived models or formulae representing output from an unshaded geologger recording on a cloud-free day (Ekstrom 2004, 2007). A location estimate based on an observed light profile that poorly fits an expected light profile would entail more error than an estimate based on close correspondence between observed and modeled data. Thus, error can be assessed based on the relationship between observed and expected light profiles and, with some ground-truthing, these goodness-of-fit parameters could serve to quantify actual location error.

To our knowledge, true template fitting has not been applied to geologger data from a small songbird. Lotek Wireless distributes a software package for template fitting called LATViewer with some of its geolocation devices. However, devices compatible with LATViewer are currently too large for most songbirds. Moreover, LATViewer is proprietary and will likely not be adapted for broader use.

Even without template-fitting methods, geologger location estimates can potentially be improved by using external environmental and geographic data. The simplest illustration of this principle might be masking off areas with unsuitable habitat (e.g., restricting terrestrial species to land surfaces). Taking this concept to its logical extreme, distribution models (i.e., niche models), where habitat suitability is mapped according to a suite of bioclimatic variables based on available occurrence data (Elith et al. 2006), could be used to differentiate likely and unlikely locations. In addition, although shading due to cloud cover is now generally regarded as a source of noise in geologger studies, with geologgers capable of full-range light recording (see above), analyses could potentially make use of archived cloud-cover distributions (available from several databases) to inform location estimates. Lastly, geologgers capable of recording data other than light readings, such as temperature and wet vs. dry conditions (now available from Migrate Technology), could further enhance geographic analyses if these readings can be spatially linked to known environmental conditions.

As more sophisticated analysis tools become available, the issue of repeatability may become an even greater concern than it is now. One way to alleviate this concern is through effective and accessible archiving of raw data, metadata, analysis parameters, and analysis results through a service such as Movebank (www.Movebank.org). Movebank is a free repository for data from individually tracked animals that allows users to manage their data, visualize movement tracks, and share their findings either with the public or certain registered users. With open-source data sharing, authors will allow others to analyze and view tracking data on their own terms, and the need for exhaustive lists of parameter settings, omitted data points, and other methodological details would be minimized by citing the online repository.

The benefits of this open-access format go beyond the issue of repeatability. Archiving of geologger data will allow reanalysis and improved quantification of location error as new software tools and calibration studies emerge, and will greatly improve the capacity for meta-analyses that exploit data from previous research efforts. Most major science-funding agencies in the United States and elsewhere now have a mandate for archiving data in a manner that makes it accessible to the scientific community and, for research based on genetic data, most scientific journals require that DNA sequences be archived and made publicly available within a reasonable time frame following publication. We advocate similar requirements for tracking data, and note that Movebank is currently developing infrastructure to accommodate light-level records from geologgers and associated data sets (S. Davidson and R. Kays, pers. comm.).

RECOMMENDATIONS AND CONCLUSIONS

Geologger tracking is still in its infancy. For this field to mature, smaller and cheaper tracking devices are needed as well as improved analysis tools that are widely (and preferably freely) available. We also need to further our understanding of how geologgers affect the birds that carry them. Although thus far geologgers are associated with reduced return rates in only a few studies (Table 1), we need more studies that provide direct comparisons of return rates of tagged and untagged individuals. Lastly, because geologger data are valuable and difficult to collect, we need to establish a culture of communal data archiving and sharing to allow meta-analyses based on data from numerous independent studies as well as reanalysis of light-level data with improved software.

Geologgers have helped resolve questions that have vexed ornithologists for decades (reviewed by McKinnon et al., in press). However, perhaps even more exciting than the results obtained thus far is the knowledge that we have only witnessed the very beginning of this new era in migration research. In coming years, geologgers will facilitate collaborative studies across species ranges and improve conservation strategies and predictive models relating bird movements to climate, weather, and land-use change. Beyond scientific advancements, geologger studies clearly demonstrating the dependence of songbirds on habitats in multiple locations and countries across the hemisphere may help foster new international relationships and improve public awareness of natural history and environmental issues.

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