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Ringing & Migration

ISSN: 0307-8698 (Print) 2159-8355 (Online) Journal homepage: http://www.tandfonline.com/loi/tram20

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RINGING & MIGRATION
https://doi.org/10.1080/03078698.2018.1521116

An effective, low-tech drop-off solution to facilitate the retrieval of data loggers in animal-tracking studies

Ruben Evens[a,b], Natalie Beenaerts[a], Eddy Ulenaers[c], Nele Witters[d] and Tom Artois[a]

[a]Hasselt University, Centre for Environmental Sciences, Research Group: Zoology, Biodiversity and Toxicology, Campus Diepenbeek, Agoralaan, Gebouw D, 3590 Diepenbeek, Belgium; [b]Swiss Ornithological Institute, Seerose 1, CH-6204, Sempach, Switzerland; [c]Agentschap Natuur en Bos, Regio Noord-Limburg, Herman Teirlinck Havenlaan 88 bus 75, 1000 Brussels, Belgium; [d]Hasselt University, Centre for Environmental Sciences, Research Group: Environmental Economics, Campus Diepenbeek, Agoralaan, Gebouw D, 3590 Diepenbeek, Belgium

ABSTRACT
Studying the movement ecology of smaller birds generally implies the use of archival devices, which require retrieval in order to download tracking data. When recapturing fails, archival devices are usually lost and birds carry the devices for longer than necessary. We present a cheap, safe and simple method to detach archival devices from animals in a semi-controlled manner. We used Eco Balloon Ribbon, a water-soluble ribbon, to attach GPS loggers to European Nightjars *Caprimulgus europaeus* via tail mounts. The ribbon was used as a weak link that dissolved within two minutes after heavy rain. The deployment duration could be estimated by following weather forecasts and the GPS loggers retrieved using a GPS-enabled radio tag. During the course of one breeding season, we deployed 44 GPS loggers and successfully retrieved 39. Here, we share our experience with Eco Balloon Ribbon, describe how to deploy a GPS logger using the tail-mount technique and provide useful tips to increase the success of drop-offs. Our methods can improve the efficacy of tracking studies, reduce the impact on the study species, and facilitate licensing and obtaining fieldwork permissions. Furthermore, we believe that Eco Balloon Ribbon has great potential to serve also in the long-term tracking of wildlife, through its integration as a weak point in collars or harnesses.

ARTICLE HISTORY
Received 5 April 2018
Accepted 21 June 2018

Scientists are pushing technological limits in their efforts to track the whereabouts of animals (Bridge *et al* 2011), in order to investigate the evolutionary and ecological processes that shape their use of space (Nathan 2008). Tracking devices and bio-loggers are now able to reveal the movement and behaviour of individuals in unprecedented detail and can provide an integrated view of the animal in its environment (Kays *et al* 2015).

In bird research, tracking devices are designed to minimise the impact on birds' survival and behaviour. Ideally they are light (3–5% body mass) (Casper 2009, Barron *et al* 2010) and with optimised aerodynamics (Bowlin *et al* 2010). The recent development of miniaturised GPS and activity loggers (Liechti *et al* 2013) allows scientists to study the movement of lightweight birds (>30 g). Miniature GPS loggers have been used in short-term (Heldbjerg *et al* 2017) and long-term tracking studies (Hallworth & Marra 2015, Evens *et al* 2017b). Attachment types vary from long term (e.g. full-body harnesses and leg loops: Evens *et al* 2017b, Hallworth & Marra 2015) and medium term (e.g. tail mounts: Vandenabeele *et al* 2014) to short term (e.g. glue mounts: Evens *et al* 2017a). For most archival devices, however, retrieval is required in order to download the data. When recapture of a tagged individual fails, the device is usually lost to the researcher and the bird carries the device for longer than necessary. Deployment of a release mechanism can avoid these problems.

Unsuccessful attempts have been made to develop reliable and safe release mechanisms, such as weak-link harnesses, surgical thread or tiny explosives. Although a safe mechanism has been developed recently (Rutz & Troscianko 2013), most other techniques still put animals at risk of entanglement or are too heavy to be suitable for smaller species (Millspaugh & Marzluff 2001, Rutz & Troscianko 2013). Since 2014, we have been using miniature GPS loggers (1.5–2 g) to study the movement behaviour of breeding European Nightjars *Caprimulgus europaeus* (mean mass around 70 g) in Flanders, Belgium. The GPS loggers are capable of a tracking bird's movement over four to ten nights, with GPS positions fixed every three minutes. Between 2014 and 2016 we deployed these GPS loggers using full-body harnesses. We retrieved only 61% of loggers, despite intensive recapture effort.

CONTACT Ruben Evens ruben.evens@uhasselt.be

To reduce the annual loss of loggers and to increase the number of birds tracked per breeding season, we tested a simple, safe and cheap method to retrieve GPS loggers via 'semi-controlled drop-off'. We show that our method can reduce the time for which birds are handled, avoid recapture attempts, minimise the annual loss of loggers and increase the amount of data collected per season. Furthermore, we anticipate that the material we used will serve purposes in many attachment types for studies on a wide range of species, even beyond the scope of tracking birds. Additionally, we anticipate that the use of this semi-controlled drop-off method can facilitate the process of obtaining licenses and fieldwork permissions for the deployment of tracking devices in wildlife studies.

Methods

GPS tracking was conducted from May to August 2017 at three sites in Flanders (Evens *et al* 2017a). Nightjars were captured using ultra-fine mist-nets (Ecotone, 12 × 3 m) and playback lures. All birds were marked with a unique alphanumeric ring from the Royal Belgian Institute of Natural Sciences. In order to maximise our chances of recovering tracking devices, we deployed loggers mainly on territorial males, breeding females and birds tracked in previous years.

Tracking devices

For this study, we combined Biotrack Ltd Pip3 Ag376 radio tags (hereafter referred to as VHF tags: 0.7 g, light potting, pulse length 20 ms, pulse rate 30/min, life span 10 weeks) with Pathtrack Ltd Nanofix GPS loggers (1.7 g) (Fig. 1). Using a very small amount of superglue gel, a VHF tag was glued onto the back of a GPS logger; hereafter the combination will be referred to as VHF/GPS logger. We made sure that the GPS module of the logger was not covered and that access to the connection pins was clear (Fig. 1). The GPS loggers were modified with a 1.5-cm extension tube at the proximal and distal ends of the logger (Fig. 1). These two extension tubes were intended to improve the stability of the logger when mounted on the shafts of the two central tail feathers (Fig. 2a).

The tags were positioned close to the bird's centre of gravity and the position on the shafts of the central tail feathers enables a safe release. We also fitted a colourful rubber balloon (0.5 x 2 cm) around the VHF/GPS logger in order to facilitate its retrieval after drop-off (Fig. 3). The combination of VHF tag, GPS logger and rubber balloon weighed 2.5–2.6 g.

To identify any possible effects of gluing a VHF tag onto a GPS logger, we assessed the performance of four stationary GPS loggers, three of them with VHF tags attached (Appendix).

Eco Balloon Ribbon

We used Eco Balloon Ribbon (patented and OEKO-TEX® certified; www.ecoballoonribbon.com) to attach a VHF/GPS logger to the tail of a Nightjar. Eco Balloon Ribbon has a woven structure and is durable and very strong when kept dry. The ribbon is 100% biodegradable and water soluble. It dissolves within two minutes when it comes into contact with water.

VHF/GPS logger attachment

Prior to deployment we activated each VHF tag's magnetic switch and tuned our Sika radio-tracking receivers to the right frequency to facilitate later retrieval of the logger. Loggers were programmed to fix GPS positions every three minutes from sundown until sunrise (i.e. from 2200 h until 0500 h GMT + 1, yielding ± 180 fixes per night). We set the GPS loggers

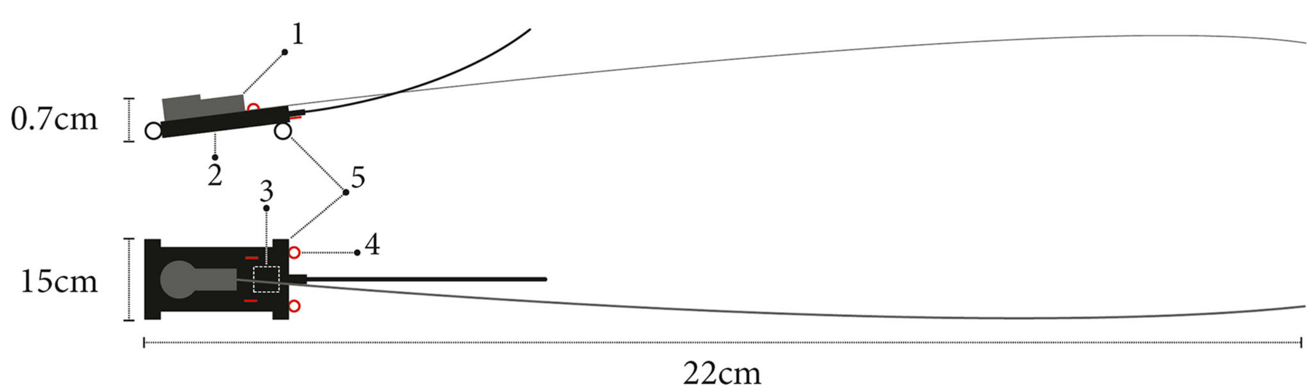

Figure 1. Schematic representation of a VHF/GPS logger. This device was built by gluing a Biotrack Ltd Pip3 Ag376 radio tag (1) to a Pathtrack Ltd Nanofix GPS logger (2). We ensured the radio tag did not cover the logger's GPS module (3) or connection pins (4). GPS loggers were modified by attaching 1.5-cm extension tubes at the proximal and distal ends (5).

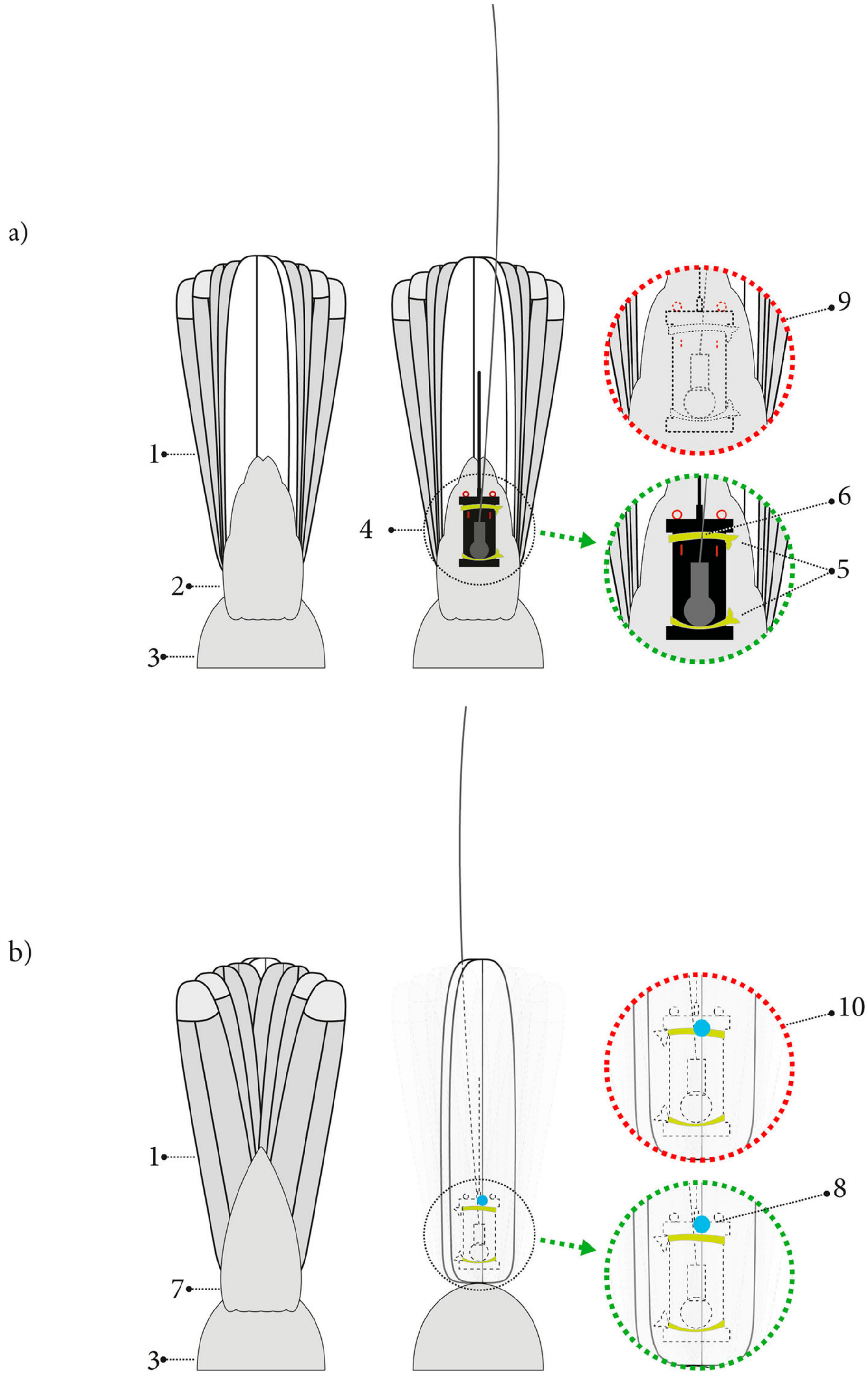

Figure 2. Schematic overview of VHF/GPS logger placement on the tail of a Nightjar: (a) top view, (b) bottom view. The tail feathers (1), upper tail-coverts (2), under tail-coverts (7) and end of the bird's body (3) are exposed for deployment of the logger. The logger is placed on the shafts of the two central tail feathers (unshaded), on top of the upper tail-coverts (4), and firmly tied at one side of the logger using two lengths of Eco Balloon Ribbon (5). The antenna of the radio tag must not be included in the distal knot (6). One drop of superglue (blue) is placed near the distal ribbon to prevent the logger from sliding off the tail (8). To assure drop-off, do not place the logger under the upper tail-coverts (9) and do not put superglue on the distal ribbon (10).

to activate five minutes after the programming finished, to avoid their software malfunctioning. Birds were released with VHF/GPS loggers within these five minutes.

To deploy the VHF/GPS logger, we first immobilised the Nightjar by wrapping it head-first into a large bird bag, leaving only the tail feathers, upper tail-coverts, under tail-coverts and end of its body exposed (Fig. 2a). Second,

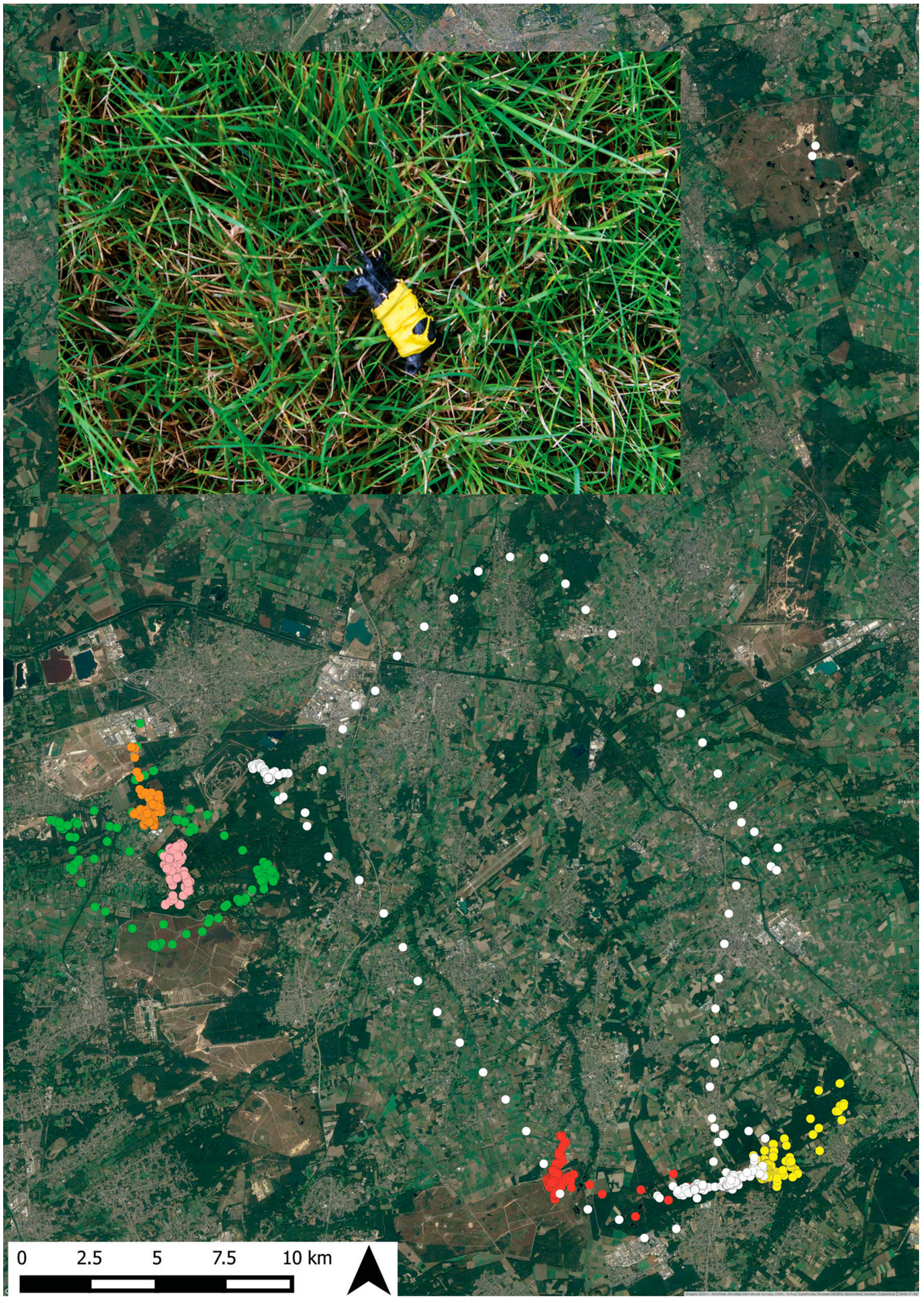

Figure 3. GPS tracks of paired and unpaired Nightjars. Each colour represents all data collected from one individual in 2017. Tracks of paired Nightjars are recognised by recursive movements between breeding and foraging habitats (orange, pink, red, yellow: range 0.5–7.5 km per night) (Evens *et al* 2017a), whereas tracks of unpaired males show movements between distant patches of breeding habitat (green: 15–35 km per night, white: 40–65 km per night). Inset shows a dropped VHF/GPS logger: a yellow balloon had been wrapped around it to facilitate its retrieval.

we isolated the upper tail-coverts and the two central tail feathers from the rest of the tail by placing a long cotton swab underneath them. Third, we lined up the central axis of the VHF/GPS logger with the gap between the shafts of the two central tail feathers (Fig. 2a). We made sure that the logger was placed close to the bird's body, on top of the upper tail-coverts. Fourth, using a long pair of tweezers, we slid two 10-cm Eco Balloon Ribbons underneath the central tail feathers. Fifth, we firmly tied the ribbons around the proximal and distal ends of the

Table 1. Overview of 44 logger deployments in 2017 and estimated time until retrieval. Logger retrieval was by drop-off except for seven birds (*) that were recaptured. Five loggers were lost.

Ring	Deployed	Site	Mount	Sex	Period (days)	GPS fixes
H02	8 May	Bosland	tail	M	7	0
G30	8 May	Meeuwen-Gruitrode	tail	M	7	1200
F12	15 May	Meeuwen-Gruitrode	harness	F	7	860
E47	15 May	Meeuwen-Gruitrode	tail	M	7	600
H05	15 May	Meeuwen-Gruitrode	tail	M	lost	
E64	15 May	Bosland	tail	M	7	600
F06	15 May	Bosland	tail	M	7	0
H09	16 May	NP Hoge Kempen	tail	M	lost	
E53	17 May	Bosland	tail	M	10	0
G66	22 May	Meeuwen-Gruitrode	tail	M	45*	1600
G69	22 May	Meeuwen-Gruitrode	tail	M	45*	1330
F08	22 May	Meeuwen-Gruitrode	tail	M	30*	1530
H17	24 May	NP Hoge Kempen	harness	F	10	0
E42	24 May	NP Hoge Kempen	tail	M	30*	1046
G23	24 May	NP Hoge Kempen	tail	M	14	966
G24	24 May	NP Hoge Kempen	tail	F	60*	1166
H24	30 May	Bosland	tail	F	lost	
953	12 Jun	Bosland	tail	F	7	740
G44	14 Jun	NP Hoge Kempen	tail	F	14	1490
H36	14 Jun	NP Hoge Kempen	tail	M	14	1507
G46	14 Jun	NP Hoge Kempen	tail	M	14	0
H38	14 Jun	Bosland	tail	F	14	980
H39	14 Jun	Bosland	tail	F	10	470
H41	15 Jun	Meeuwen-Gruitrode	tail	M	14	1387
H44	26 Jun	Meeuwen-Gruitrode	tail	M	10	0
H45	28 Jun	Bosland	tail	M	60*	705
G51	28 Jun	Bosland	tail	M	60*	1099
G32	3 Jul	Meeuwen-Gruitrode	tail	M	14	1243
H23	3 Jul	Meeuwen-Gruitrode	tail	M	14	715
H43	3 Jul	Meeuwen-Gruitrode	tail	M	14	1580
H48	4 Jul	Kalmthout	tail	M	2	180
F19	8 Jul	NP Hoge Kempen	tail	M	10	931
H56	20 Jul	NP Hoge Kempen	tail	M	5	300
H57	20 Jul	NP Hoge Kempen	tail	M	5	300
H58	20 Jul	NP Hoge Kempen	tail	M	lost	
E59	21 Jul	Bosland	tail	F	3	180
H62	26 Jul	NP Hoge Kempen	tail	M	6	400
997	26 Jul	NP Hoge Kempen	tail	F	6	750
H63	31 Jul	Bosland	tail	F	3	450
H68	3 Aug	NP Hoge Kempen	tail	F	5	50
H69	3 Aug	NP Hoge Kempen	tail	M	5	450
H71	3 Aug	NP Hoge Kempen	tail	F	lost	
H72	3 Aug	NP Hoge Kempen	tail	F	5	450
G60	7 Aug	Bosland	tail	F	5	400

logger using a triple knot (Fig. 2a). Two extension tubes facilitated the secure tying of the ribbon and allowed the position of the logger to be adjusted. We checked that all upper tail-coverts were still under the logger, that the knots were positioned to the side of the logger (Fig. 2a) and that we had avoided tying the antenna of the VHF tag to the logger (Fig. 2a). Sixth, to prevent the logger from sliding down the tail, we placed one drop of Bison Superglue Gel at the underside on the shaft of the lower central tail feather (Fig. 2b). We tried to place the drop of glue at least 2 mm from the distal Eco Balloon Ribbon. Finally, we trimmed the remaining Eco Balloon Ribbon and released the bird.

VHF/GPS logger retrieval

We monitored local weather forecasts to ensure that VHF/GPS loggers were deployed at least four nights before rains were predicted. Twelve hours after deployment, we located the roosting and breeding sites of each tagged bird. When heavy rains occurred during daytime, the VHF/GPS loggers could then be easily collected at these sites. When rains occurred at night, the tags could have been dropped off close to breeding or roosting sites, or at distant foraging sites (Evens *et al* 2017a). In the latter case, wide-ranging searches were required to retrieve the loggers.

Results

Retrieval of data

We retrieved 89% (39 out of 44) of our VHF/GPS loggers, of which 32 dropped off as planned (Table 1). From the five loggers we lost, one logger dropped off in an inaccessible military area and four at unknown locations. The latter group had probably been deployed on unpaired males and could not be relocated, even after a wide-ranging aerial search (Fig. 3).

Due to the experimental nature of the attachment methods, drop-off failed for seven individuals. The reasons for these failures are described below. We retrieved these seven loggers by recapturing the Nightjars. From these seven loggers, five were still glued to the tail feathers. These loggers were still in the same position on the birds as when they were deployed and the birds themselves showed no sign of any negative effects of carrying the loggers. Two other loggers had been deployed as harnesses (see below).

Among the loggers retrieved, two had not collected tracking data due to unexpected rains in the night following deployment. For five other loggers, no tracking data were recorded, due to programming issues. The VHF tag did not reduce the performance of the GPS logger (see Appendix).

The time between deployment and successful drop-off ranged from one to 30 days ($n = 32$, mean $= 10 \pm 7$ days). Owing to our new attachment method, we were able to perform almost as many deployments in one season (2017: 44 deployments, with 25 loggers) as we had in the three previous seasons combined (2014–16: 49, with 49 loggers). Furthermore, we lost fewer loggers (2017: 11% loss vs. 2014–16: 39%) and collected more tracking data (2017: 27 600 observations vs. 2014–16: 16 400 in total).

Points requiring attention

It is essential to prevent feathers covering the Eco Balloon Ribbon, as this can inhibit contact between rain and the ribbon. We illustrate this with two examples. Firstly, we deployed two VHF/GPS loggers as a backpack with full-body harness following the methods described by Evens *et al* (2017b). Both loggers were deployed one week prior to heavy rains and success of the drop-off was checked immediately after the rains occurred. Although the rear parts of the harnesses had disintegrated, the forward parts had not, leaving the VHF/GPS loggers hanging as necklaces around the birds' necks. Both loggers were recovered the same evening by trapping the birds. Examination of these harnesses showed no disintegration of the ribbon, suggesting that the Nightjar's plumage is very water repellent. Following these observations, we do not recommend using the ribbon as a body harness on birds that, for example, have a thick plumage or do not wet their feathers when bathing. Secondly, we deployed four tail-mounted VHF/GPS loggers by placing the loggers under the upper tail-coverts (Fig. 2a). Similarly, the upper tail-coverts also prevented the successful, swift disintegration of the proximal Eco Balloon Ribbon. Eventually, two loggers dropped off one month after deployment and two VHF/GPS loggers were recovered by recapturing the birds.

We noticed that the triple knots do not disintegrate as quickly as the ribbons that run over or under the loggers. Therefore, we recommend that the knots should be positioned to one side (left or right) of the loggers (Fig. 2a). When rains occur, this allows swift disintegration of the ribbon and detachment of the tag, even when the knots do not disintegrate entirely.

Correct placement of the superglue gel is essential. Superglue gel is less likely to flow than regular superglue and so less likely to touch the Eco Balloon Ribbon (Fig. 2b) and soak into the woven structure. When this happens, the superglue sets and will prevent the disintegration of the ribbon. We incorrectly positioned the superglue for three loggers and needed to recapture these birds.

Conclusion

During the course of one breeding season (May–August 2017), we have developed a very simple method to enable the semi-controlled drop-off of VHF/GPS loggers to study the movement ecology of a lightweight bird. These loggers were attached to Nightjars as tail mounts using a water-soluble ribbon, Eco Balloon Ribbon. This attachment method does not seem to influence the birds' behaviour, manoeuvrability or comfort. The ribbon dissolved within two minutes after heavy rain, thus detaching the loggers from the birds. We could then retrieve the loggers by tracking the VHF signal.

Owing to this efficient method, we reduced the handling time for logger attachment to less than five minutes and, for deployments that were executed well, we were no longer obliged to recapture the birds to retrieve their loggers. Furthermore, we reduced the annual loss of loggers, doubled the number of tracked birds and dramatically increased the tracking data that were collected during one season. Our method has thus improved the efficacy of our study through an increase in the yield of tracking data and a reduced project cost, with fewer devices consumed and less time invested in retrieving loggers.

Eco Balloon Ribbon is strong, durable when kept dry, and very cheap (250 m for 70€). We anticipate that the applicability of Eco Balloon Ribbon can go beyond the short-term tracking of lightweight birds. For example, manufacturers of tracking equipment could integrate this ribbon as a weak point in harnesses or collars. Furthermore, we hope other researchers can use this proof of concept to facilitate the process of obtaining licences and fieldwork permissions.

Acknowledgements

RE was funded by a BOF-mandate (BSFFCMKDK) at Hasselt University. NW was funded as a postdoctoral researcher by FWO Flanders. We thank Luc Lens, Dries Gorissen, Guido Winters, Koen Thijs, Lise Hendrick, Karen Vanmarcke, Fien Evens, Albert Geuens, Lyndon Kearsley, Greg Conway, Ian Henderson and Nikki Watson for their support and for relevant comments on this manuscript. Research equipment was funded by the Agency for Nature and Forest (ANB) (Belgium). Permissions were granted by the ANB and the Royal Belgian Institute of Natural Sciences.

References

Barron, D.G., Brawn, J.D. & Weatherhead, P.J. (2010) Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* **1**, 180–187. doi:10.1111/j.2041-210X.2010.00013.x

Bowlin, M.S., Henningsson, P., Muijres, F.T., Vleugels, R.H.E., Liechti, F. & Hedenström, A. (2010) The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods in Ecology and Evolution* **1**, 398–402. doi:10.1111/j.2041-210X.2010.00043.x

Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Kays, R., Kelly, J.F., Robinson, W.D. & Wikelski, M. (2011) Technology on the move: recent and forthcoming innovations for tracking migratory birds. *BioScience* **61**, 689–698. doi:10.1525/bio.2011.61.9.7

Casper, R.M. (2009) Guidelines for the instrumentation of wild birds and mammals. *Animal Behaviour* **78**, 1477–1483. doi:10.1016/j.anbehav.2009.09.023

Evens, R., Beenaerts, N., Witters, N. & Artois, T. (2017a) Study on the foraging behaviour of the European Nightjar *Caprimulgus europaeus* reveals the need for a change in conservation strategy in Belgium. *Journal of Avian Biology* **48**, 1238–1245. doi:10.1111/jav.00996

Evens, R., Conway, G.J., Henderson, I.G., Cresswell, B., Jiguet, F., Moussy, C., Sénécal, D., Witters, N., Beenaerts, N. & Artois, T. (2017b) Migratory pathways, stopover zones and wintering destinations of Western European Nightjars *Caprimulgus europaeus*. *Ibis* **159**, 680–686. doi:10.1111/ibi.12469

Hallworth, M.T. & Marra, P.P. (2015) Miniaturized GPS tags identify non-breeding territories of a small breeding migratory songbird. *Scientific Reports* **5**, 11069. doi:10.1038/srep11069

Heldbjerg, H., Fox, A.D., Thellesen, P.V., Dalby, L. & Sunde, P. (2017) Common Starlings (*Sturnus vulgaris*) increasingly select for grazed areas with increasing distance-to-nest. *PLoS ONE* **12**, e0182504. doi:10.1371/journal.pone.0182504

Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an eye on life and planet. *Science* **348**, 1222–1232. doi:10.1126/science.aaa2478

Liechti, F., Witvliet, W., Weber, R. & Bächler, E. (2013) First evidence of a 200-day non-stop flight in a bird. *Nature Communications* **4**, 2554. doi:10.1038/ncomms3554

Millspaugh, J.J. & Marzluff, J.M. (2001) Radio-tracking and animal populations: past trends and future needs. In *Radio Tracking and Animal Populations* (eds Millspaugh, J.J. & Marzluff, J.M.), 383–393. Academic Press, London.

Nathan, R. (2008) An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences* **105**, 19050–19051. doi:10.1073/pnas.0808918105

Rutz, C. & Troscianko, J. (2013) Programmable, miniature video-loggers for deployment on wild birds and other wildlife. *Methods in Ecology and Evolution* **4**, 114–122. doi:10.1111/2041-210x.12003

Vandenabeele, S.P., Grundy, E., Friswell, M.I., Grogan, A., Votier, S.C. & Wilson, R.P. (2014) Excess baggage for birds: inappropriate placement of tags on gannets changes flight patterns. *PLoS ONE* **9**, e0092657. doi:10.1371/journal.pone.0092657

Appendix: Performance of VHF/GPS loggers

We assessed the performance of four stationary loggers (three VHF/GPS loggers, one GPS logger) to identify the effect of gluing a VHF tag onto a GPS logger. The loggers were placed in an open field, one metre above ground level and one metre from each other. All loggers were activated at the same time and logged GPS positions at the same interval as used during the study (three minutes). We used ANOVAs to calculate differences in the detection of satellites, the accuracy indicator provided for each GPS fix and the distance of estimated GPS positions from the exact location of deployment.

The GPS logger collected 1324 observations and the VHF/GPS loggers collected 1517, 1318 and 1273 observations. Analysis of the loggers showed that VHF/GPS loggers received the same number of satellites compared with the GPS logger ($df_N = 3$, $df_D = 5428$, $F = 0.976$, $P = 0.403$) (Fig. A1).

Accuracy was significantly different between loggers ($df_N = 3$, $df_D = 5428$, $F = 4.746$, $P = 0.0026$), with one VHF/GPS logger (VHF/GPS 3) more accurate than the GPS logger (Tukey-adjusted pairwise comparison, $\mu_{diff} = 3.12^{-7}$, df = 5428, $P = 0.002$). All loggers performed similarly in terms of the difference calculated between the estimated longitude and true deployment location ($df_N = 3$, $df_D = 5428$, $F = 0.08$, $P = 0.971$). There was only a slight difference in the estimation of latitude ($df_N = 3$, $df_D = 5428$, $F = 5.19$, $P = 0.0014$), where VHF/GPS 2 was more accurate than VHF/GPS 1 (Tukey-adjusted pairwise comparison, $\mu_{diff} = -2.38^{-7}$, df = 5428, $P = 0.002$) and VHF/GPS 3 (Tukey-adjusted pairwise comparison, $\mu_{diff} = -1.87^{-5}$, df = 5428, $P = 0.033$) (Fig. A2).

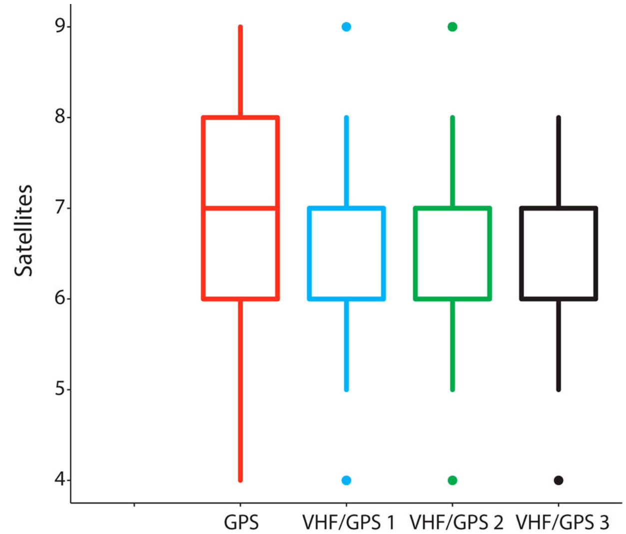

Figure A1. Boxplots showing the number of received satellites for each observation per logger. Boxplots show the median (central horizontal line in case of GPS), quartiles (box), 90% range (whiskers) and outliers.

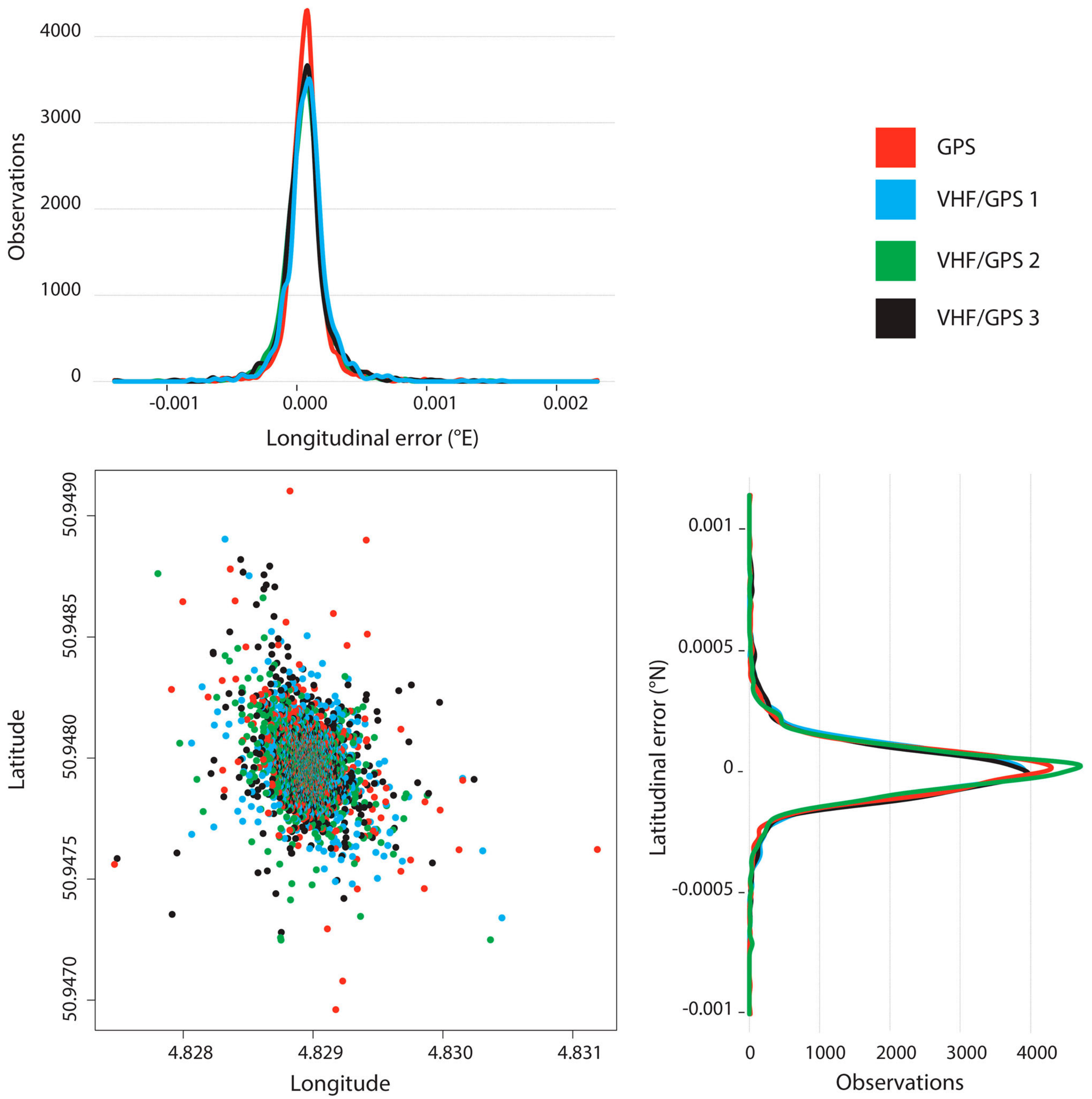

Figure A2. Scatter of GPS fixes for each logger, plotted by colour, with the distributions of longitudinal and latitudinal errors between the observed and true deployment locations.