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REVIEW

50 years of bat tracking: device attachment and future directions

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Summary

1. Radiotelemetry and satellite-based telemetry approaches are essential to describe the behaviour and biology of animals. This is especially true for bats, whose small size and cryptic lifestyles make them challenging to study. However, only a handful of studies have evaluated how transmitter mass and the attachment method affect bat behaviour or health, and none have assessed the development of technical methods in the field.

2. We review the past 50 years of bat tracking studies to determine how devices have been attached, how guidelines have been followed or changed, and whether any health or fitness impacts from these transmitters can be determined.

3. Half of the nearly 300 studies available used devices heavier than the recommended 5% of body mass with minimal justification. Devices were typically glued directly to the backs of small bats and remained attached for 9 days. This is far shorter than battery life span of most devices. Little information is available regarding the overall impact of attaching transmitters on the health, survival and reproductive success of bats, and there has been little development in attachment methods since the first tracking studies.

4. We consequently developed a collar for small bats with a degradable weak link and tested it on several species. The collar worked successfully on three of four species. This allows longer habituation and tracking times while ensuring that the device drops off after the battery expires.

5. Future studies will need to invest more effort in assessing potential long-term effects of tracking. They also need to build upon previous knowledge to find the best attachment method, size and shape for their study species to effectively improve wildlife tracking.

Key-words: radiotracking, telemetry, GPS tracking, movement, 5% rule

Introduction

Wildlife tracking has made invaluable contributions to our understanding of animal behaviour and ecology. It is essential to data collection of animal movement and migration, and remote tracking is often the only method that can replicate or replace laboratory work with studies conducted in the wild (Joslin, Fletcher & Emlen 1964; Blanchard, Flannelly & Blanchard 1986; Calisi & Bentley 2009; Tomotani *et al.* 2012). Limited studies have evaluated the efficacy of attachment types, durations and the effects of attached transmitters on animal welfare (reviewed in: Murray & Fuller 2000), and flying animals are thought to be particularly sensitive to the added weight of a device (Cochran 1980; Caccamise & Hedin 1985). In birds, transmitters often have significant negative effects on nearly all aspects of their biology, with the major exception of flying ability (Barron, Brawn & Weatherhead 2010). However, how much these results can be generalized is unclear. Bats are the only other vertebrates capable of powered flight, and unlike birds, flying ability and manoeuvrability are significantly affected by increased loading under conventional guidelines (e.g. (Rayner, Jones & Hughes 1987; Aldridge & Brigham 1988; Hughes & Rayner 1991; Macayeal *et al.* 2011; Iriarte-Diaz *et al.* 2012), but long-term effects of carrying transmitters are unknown. Because of the importance of telemetry to understanding bat biology, it is essential to understand how prevalent various device attachment methods are, how long devices stay attached and what effect transmitters have on bat biology and behaviour.

Bats are not only difficult to study because they fly and are primarily active at night, but their small size, expensive flight cost, and rapid heat and water loss (Speakman & Thomas 2003) all make carrying the additional mass of a transmitter problematic. Their cryptic lifestyles have made radiotelemetry essential to describe many aspects of their lives, from foraging behaviour to social organization to physiology. Improvements in tracking methods, particularly in how devices are attached,

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would expand our ability to study the complex behaviour and biology of these elusive animals and greatly add to the knowledge gained by past tracking and telemetry studies (Davis & Cockrum 1964; Bradbury 1977; Bradbury *et al.* 1979; Petit & Mayer 1999; Willis & Brigham 2003; Richter & Cumming 2008; Amelon *et al.* 2009; Stawski, Turbill & Geiser 2009; Smith *et al.* 2011; Tsoar *et al.* 2011; Roberts *et al.* 2012).

Some authors have suggested that an attached transmitter should not exceed 10% of a bat's body mass (Wilkinson & Bradbury 1988; Sikes & Gannon 2011) and preferably less. Aldridge & Brigham (1988) suggested that bats under 70 g (i.e. the vast majority of species) should carry no more than 5% of their body mass, a value that has become *de facto* best practice. Their study showed that adding weight to the 6·0 g *Myotis yumanensis* linearly decreases manoeuvrability through cluttered artificial habitats. However, a comparative study of morphologically similar bats showed that body size had the strongest effect on manoeuvrability, along with wing camber (Stockwell 2001), with larger bats less able to manoeuvre through increasingly complex environments. The results of these studies indicate that a linear scaling across species of body mass with transmitter mass may be too simplistic.

While the effect of the payload carried by a bat has received some attention, there has been little work to understand the effects and challenges of attaching such devices to bats. Birds typically have transmitters glued to their dorsum or tail feathers, or secured with a backpack harness. Backpack-type harnesses cannot be used on bats as it would require cutting through the wing membrane that attaches along the leg and often is attached to the heel of the foot. The most common method of device attachment is to glue the transmitter to the bats' dorsal fur with a variety of adhesives, with or without clipping the dorsal fur beforehand. This ensures that the transmitter will eventually fall off of the study animal, but recovering the device may not be possible. Once the bat with the glued transmitter is released, it is impossible to control how long the device remains attached. Researchers often initiate data collection soon after release to gather as much data as possible before the transmitter falls off or is removed by the bat, but typically wait until the second night after attachment to collect data (Audet & Fenton 1988). The stress of capture, handling and device attachment may have strong short-term influences on the animal's behaviour (e.g. increase vigilance and decrease foraging), and thus, the data collected soon after release may not be an accurate representation of an individual's behaviour (Kenward 2000). This effect is further enhanced if the overall period of tracking is short because of the limited time, the transmitter remains attached.

To gain an overview of past developments and current practices in tracking studies, we reviewed the published literature to identify how long devices are staying attached, the relative mass of devices used, the attachment method, and impact of the transmitter on bat health and biology. We then present a lightweight collar attachment method with a degradable weak link that significantly extends device attachment while providing a predictable time frame for the device's removal.

Literature review

We conducted our literature search through Web of Science. The key words 'bat' and 'radiotracking' or 'radiotelemetry' as well as 'bat' and 'satellite', 'GPS', and 'tracking' were used current to 15 January 2013. We also included references cited within the resulting publications as well as those that directly cited Aldridge and Brigham (1988). We supplemented this data set with direct searches of the Journal of Mammalogy and Acta Chiropterologica (two journals where studies of basic bat biology are frequently published) using the same terms, and publications from our own knowledge that were not returned by either literature search. While this may have missed some studies, the use and diversity of methods should be well represented in the citations returned.

From the resulting publications, we extracted data on the species studied, study location (temperate or tropics/subtropics), body mass, type of device used (radiotransmitter, GPS transmitter, or GPS logger), the relative and absolute tracking device mass, attachment method (glue/collar/other, whether fur was trimmed at attachment site, type of adhesive used), the duration of attachment and the duration of tracking. Because few studies were complete in these variables, we estimated several parameters. We substituted the range of species masses when body mass of the individuals studied was not reported. As a conservative estimate, if relative device mass was <5% of the minimum possible mass for the bat species in question, it was considered heavier than 5%. Duration of attachment was not always listed, especially in cases where tracking was stopped before the device fell off. When a range of attachment durations was given, the mid-point of that range was taken. Additionally, our goal was to extract data on the effects of transmitters on bat health, life span and reproductive success (*sensu* Barron, Brawn & Weatherhead 2010). However, few authors reported post-tracking data or changes in body mass, annual reproductive output or had designed studies that directly addressed these questions. Because of the small sample size, we could not analyse transmitter effects in a quantitative way, but describe these individual studies in the discussion.

Results – literature search

Two hundred and eighty-one transmitter deployment studies from 222 citations on 128 species or subspecies of bats were returned in our literature search. These studies attached a radiotransmitter ($n = 273$), satellite transmitter ($n = 8$) or GPS data logger ($n = 1$). For ease of discussion, we include all tracking devices under 'transmitter'. In 239 of the deployment studies, researchers glued transmitters directly to the skin or fur on the bat's back, 34 used some type of collar attachment and nine studies either did not report how the transmitter was attached or used another method (e.g. peritoneal implant). Studies that reported the duration of attachment showed that transmitters on collars remained attached longer than those with adhesive (Table 1).

Table 1. Duration of attachment (days ± SE) for transmitters attached by collars or adhesive directly to bat's skin or fur (where reported)

	Collar	Adhesive
Duration of attachment	163·1 ± 13·2	9·3 ± 4·6
Range of attachment	3–365+	1–90
Number of cases	19	154

RELATIVE TRANSMITTER MASS

Our analysis of relative transmitter mass is confounded by the lack of direct reporting of body or transmitter mass by many studies. While it is standard to indicate that body mass and forearm length (a proxy for body size) were taken for each individual bat, only 46% of studies report the actual values. Instead, some cite a species mass range. Many fail to report body masses entirely and merely denote that the transmitters were a given percentage of individual body mass.

Consequently, we were only able to identify average relative transmitter mass in 148 cases. One hundred and forty-five studies (98%) used transmitters that weighed <10% of the bat's body mass, but only 51% (74 studies) used transmitters that weighed <5%. Studies that exceeded the 5% guideline did so with minimal justification relative to the study species' behaviour, anatomy or health. The most commonly used justification was that previous studies had attached similar weights. However, a few authors also provided a thorough justification for the use of transmitters up to 10% of the study species' body mass, based on foraging patterns, manoeuvrability, wing loading and/or post-tracking recapture to inspect the health of the study animals (e.g. Weinbeer, Meyer & Kalko 2006; Patriquin *et al.* 2010).

ATTACHMENT METHODS: GLUE

Directly gluing transmitters was by far the most common method (Table 1), and devices typically remained attached for fewer than 10 days. 84·7% of the studies using radiotransmitters glued them on to the bats. This covers approximately one-third to one-half of the potential battery life and poses significant time constraints on the flexibility of studies and the post-handling recovery and habituation period to the transmitter. Furthermore, duration of attachment seemed to be species-dependent. For example, the average duration of attachment on bats from the family Molossidae was 6·5 ± 3·8 days (Table 2), but even shorter attachment times of 1–3 days have been reported for *Molossus molossus* and *Tadarida australis* (Rhodes *et al.* 2006; Dechmann *et al.* 2010; Holland *et al.* 2011). In contrast, the one tracked hipposiderid species tolerated the glued-on transmitters for 30 days, although this was during its hibernation period (Liu & Karasov 2011). These differences may be due to any combination of species' or individual temperament and activity level, morphological restrictions, differences in attachment method details (e.g. adhesive used), as well variability in researchers' skills in attaching the transmitter.

Table 2. Duration (days ± SE) for transmitter attachment in represented bat families

Family	N Studies	Duration
Hipposideridae	1	30·0
Molossidae	7	6·6 ± 3·8
Mystacinidae	2	7·2 ± 7·2
Noctilionidae	2	7 ± 7·2
Phyllostomidae	40	9·2 ± 1·6
Pteropodidae	5	11·9 ± 4·5
Rhinolophidae	6	5·8 ± 4·1
Vespertilionidae	92	9·8 ± 1·1

Multiple types of adhesive, from latex-based surgical glue (e.g. Skin Bond or Osto Bond, Smith and Nephew Products, Inc., Largo, FL USA) to cyanoacrylates, have been used with varying degrees of effectiveness. One hundred and sixty-seven of the 269 cases used latex-based surgical glue to glue the transmitter either to the fur or skin of bats after clipping the fur. There is no significant difference in the mean duration of glue attachment between the temperate and tropical zones ($t = 1{\cdot}078$, d.f. = 136, $P = 0{\cdot}282$), but transmitters stay attached an average of one day longer in the temperate zones, with a much longer maximum range of duration (attachments of up to 90 days). Maximum duration of attachment in the tropics was 28 days (Fig. 1; Table 3).

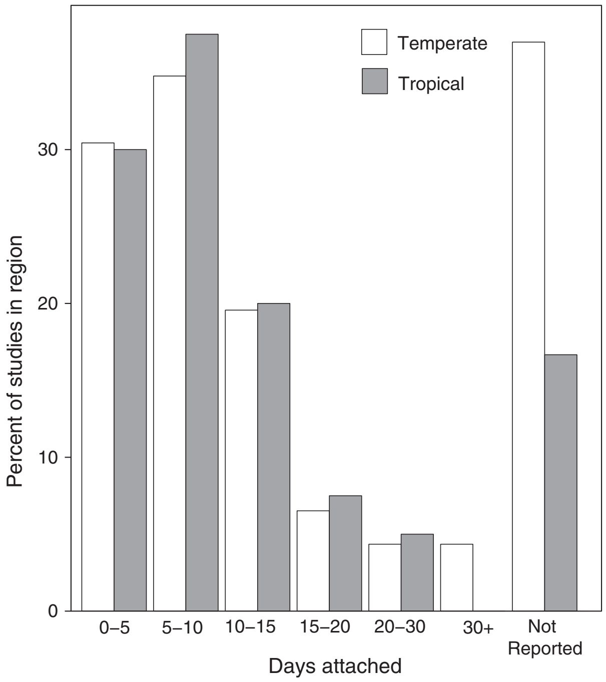

Fig. 1. Duration of transmitter attachment in temperate and tropical studies as a percentage of the total studies in each region, excluding those studies where data were not available. Studies where data were not reported are presented as a percentage of the total number of studies returned in the search.

Table 3. Duration of attachment (days ± SE) for transmitters on species in the temperate vs. tropical zone.

	Temperate	Tropics
Duration of attachment	9·9 ± 1·2	8·4 ± 0·748
Range of attachment	2–90	2–28
Number of cases	95	59

ATTACHMENT METHODS: COLLARS

Collars were rarely used and then primarily on flying foxes of 50 g or larger. Most collars were permanently attached, had various sizes and shapes and were made of leather or plastic (Smith *et al.* 2011). Flying foxes are most commonly tracked with satellite transmitters or GPS loggers that can operate for extended periods of time. There were also a few studies on smaller bats such as *Tadarida* and *Megaderma* that used permanently attached collars (Audet *et al.* 1991). Only 13 cases used a weak link or incorporated material (e.g. rubber and cotton) that degrades over several weeks or months, to ensure that the collar would fall off (Mildenstein *et al.* 2005; Rhodes 2007), with the remaining studies attaching permanent collars that can outlast potential battery life.

Collar development

Given the poor results we found in the literature regarding battery life span relative to transmitter attachment duration, we were surprised by the lack of progress in improving attachment methods. To fill this gap, we wanted to develop a collar that was safe for bats to wear, would stay on just long enough to make full use of battery life span, and that was easy to replicate and attach. Our aim was to allow for longer habituation periods, as well as collection of better quality data across greater time periods, and potentially to reduce the number of individual bats that must be tagged. Given that bats cannot easily be recaptured to retrieve the transmitter, these are single-use devices, even if battery power has not been exhausted by the time the device drops off.

We decided on a soft collar with a weak link that would eventually degrade and detach from the bat. For the collar, we tested Tyvek material (DuPont, Wilmington, USA), felt, thick rubber bands, and cotton shoelaces. The collars were glued together with cyanoacrylate glue (Kola Loka/Krazy Glue Inc., New York, NY USA) or were tied together directly on the bats using cotton thread, rubber bands or degradable suture material (Safil C synthetic polyglycolic acid thread, Aesculap/B. Braun, Co, Tuttlingen, Germany). Closure material was passed through the end of the collar using either a needle (thread & suture) or opening a small hole (rubber band). Safil C reports tensile strength loss of 50% at 18 days and 100% loss at 28–35 days. Threads were tied so that the material was passed under the two collar ends and in contact with the bats' skin and closed with a stack of square knots in one point to prevent slippage (Fig 2). Material for the collars and closures was chosen so that the collar, closure or both would naturally degrade. Some materials were represented in the literature (e.g. rubber bands), while others (e.g. Tyvek, Safil-C) had not been previously used or identified in the literature search and could represent significant improvements over previous designs. Collar length was adjusted individually so that it seemed comfortable but snug to prevent the bat from pulling the collar off enough to chew on it. To attach the collar, one person gently restrained a fully alert bat, while another carefully attached a collar to its neck. We chose not to anaesthetize our study animals, as all of them are small (<45 g) and can be carefully and safely handled by trained personnel. We wanted to find a collar solution that is easy to attach in the field and that would allow quick release of bats after capture.

STEPWISE TESTING PROTOCOL

Given the taxon-specific published differences in attachment durations (Table 2), we wanted to test our collar on taxonomically and morphologically diverse species to get an idea of the general applicability of the method. To do this, we first chose two closely related frugivores in Gamboa, Panamá, which are common, have similar foraging ecology and morphology, but

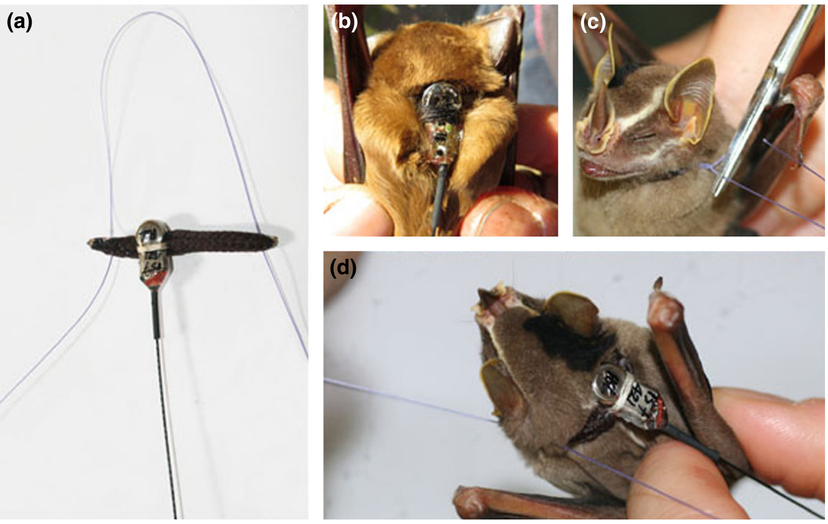

Fig. 2. Radiotransmitter and collar with suture material passed through the collar ends, ready for attachment (a); attachment on *Nyctalus noctula* (b); and *Uroderma bilobatum* (c, d).

differ in size: *Artibeus jamaicensis* (also used in the manoeuvrability study of Stockwell 2001) and *Uroderma bilobatum*. We then applied the best resulting collar on two narrow-winged insectivorous species, whose morphology, ecology and roosting behaviour varied greatly from the two frugivorous bats. The first of these two species, *Molossus molossus*, is also Neotropical and had presented a challenge for device attachment in the past. Individuals of this species remove transmitters in <3 days and in some cases <1 h (Dechmann, unpublished data). All three Neotropical bat species were tested from May to July 2012 in Gamboa, Panamá (9°6·934′N, 79°41·968′W). The second narrow-winged species was larger (25–40 g) with a large distribution in the temperate zone: *Nyctalus noctula*. This migratory species hibernates in Central Europe, and we caught our study subjects in bat boxes in Kreuzlingen, Switzerland (47°39·00′N, 9°11·11′E), and using a hand net at emergence in Konstanz, Germany (47°41·55′N, 9°07·07′E), in May 2012 and April 2013 between hibernation and the onset of migration.

We performed the initial tests of a variety of collar designs on nine adult male *Artibeus jamaicensus* (body mass: 44·3 ± 3·2 g). Two to three individuals at a time were released together into a 5 m × 3 m × 2 m tent and were held in captivity for 2–6 weeks, depending on the duration of collar attachment. Bats were fed a mix of fresh fruit with *ad libitum* access to water. Health condition and mass were monitored daily for the first week of each test and then every 2 days afterwards. Bats were allowed to acclimate to captivity for two nights before being fitted with a collar prototype.

We then tested whether the *A. jamaicensis* collar could be sized down to fit a smaller, similar species during field tracking. We used the best resulting collar in a radiotracking study of three lactating and one post-lactating female *Uroderma bilobatum* (body mass: 17·5 ± 1·5 g). Bats were captured with hand nets at their roost and were fitted with a 2·5-mm-diameter shoelace collar and a 0·85 g radiotransmitter (LB-2, Holohil Systems, Ltd). The radiotransmitter was attached to the collar with a small amount of cyanoacrylate glue (Kola Loka/Krazy Glue Inc., New York, NY USA) and then secured in place with needle and cotton thread (Fig. 2A). Total attachment mass was 0·87 g or between 4·0 and 5·1% of the body mass of these animals.

The next step was to test the generality of our collar on *Molossus molossus,* the smaller species that has consistently removed glued-on transmitters in the past. We tested rubber band and nylon ribbon as collar materials on 16 adult *M. molossus* (body mass: 12·3 ± 0·5 g) in captivity. We could not find shoelaces thin and flat enough to replicate the collars used in the *Artibeus* and *Uroderma* studies. To find an acceptable alternative for this small species, we chose to substitute rubber band and flat ribbon as replacements, keeping the degradable suture as it was previously successful. Bats were housed with their roost-mates in small tents (1 m × 0·5 m × 0·4 m) for two to seven nights and were fed mealworms (*Tenebrio molitor*) until satiated every evening. Water was available *ad libitum*. Health condition and mass of the bats were monitored nightly, and bats were released at their capture site after testing.

Lastly, we tested the final collar design in a tracking study of the European species *Nyctalus noctula* to compare with previous tracking data that used glued-on transmitters. Baseline data from glued transmitters came from 16 individuals (10 females: 27·9 ± 2·5 g, 6 males: 27·4 ± 2·9 g) in 2012 that had a 0·5 g radiotransmitter (LB2, battery life *c.* 22 days, Holohil Systems, Ltd) glued to their clipped dorsal fur. We used a silicone-based skin glue (Sauer Hautkleber, Manfred Sauer, Germany) to attach two of the radiotransmitters. Because one of the bats removed the transmitter in the first night, all remaining 14 transmitters were attached with superglue. In spring 2013, we then tracked 18 individuals (8 females: 26·9 ± 2·9 g, 10 males: 25·7 ± 2·9 g). These bats wore a 0·9 g radiotransmitter (LB2 with maximized power, battery life *c.* 21 days, Holohil Systems, Ltd) mounted on a 2·0 mm-wide shoelace collar closed with Safil-C degradable suture for a total device mass of 0·92 g. In both years, bats were tracked nightly until the transmitter fell off, or the bat migrated (i.e. the bat was followed out of the area and disappeared) or the battery life was exhausted. We used the night of last contact with a flying animal as an estimate of attachment duration. Transmitters that were not found after 20 days or more may have been on migrating individuals or their battery may have expired, making these conservative estimates. When a transmitter did not emerge from a roost for two consecutive nights, we assumed that it was not on the bat anymore. Many transmitters' batteries lasted beyond the number of days predicted by the manufacturer, allowing us to continue tracking longer than anticipated.

All work in Panamá was approved by the Autoridad Nacional del Ambiente (SE/A72-12, SE/A23-13) and the Institutional Animal Care and Use Committee at the Smithsonian Tropical Research Institute (2012·0505·2015). Work in Switzerland was approved by the Veterinäramt Thurgau (UniKN1/13), and work in Germany was approved by Regierungspräsidum Freiburg (35-9185·81/G-12/16). All methods conformed to the ASAB/ABS Guidelines for the Use of Animals in Research.

Results – collar development

BAT BEHAVIOUR AFTER COLLAR ATTACHMENT

After we placed the collars on *A. jamaicensis*, the bats readily flew away into a corner in the flight tent. They then used their feet to pull at the collar, often wetting their foot with saliva and pulling downward at the collar. Some bats continued this for nearly an hour, after which they stopped, rested and fed. Bats were observed continuously for the first hour and checked hourly until they removed the collar or six hours had passed. While we did not see bats attempt to remove their collars after the first night, the bats must have continued to pull at their collars because some designs detached after 2–7 nights, while others stayed attached longer than 1 month. All bats appeared healthy and maintained or gained weight while in captivity.

Felt collars were removed by the bats quickly (within 30 min) regardless of the closing method. Collars made of rubber band or secured with rubber bands (as had been used previously on *Tadarida*; Rhodes *et al.* 2006) were removed by *A. jamaicensis* within 1–3 h. The rubber band and felt both stretched enough to allow bats to pull the collar down from their neck and chew it off. The Tyvek material did not stretch but bunched into a tight thread. Tyvek collars that were tied on with both the suture and cotton thread were removed within 1 week (4 ± 2 days), due to the closure threads tearing through the Tyvek when bats pulled on their collars.

We then tested cotton shoelaces secured with glue (n = 1), degradable suture (n = 2) and cotton thread (n = 2). Both degradable suture and cotton thread were passed through the ends of the collar using a sewing needle and then closed while in place on the bat with a series of square knots to prevent slippage. After 3 weeks, all of the cotton shoelace collars began to fray slightly as did the cotton thread, but there were no other visible signs of degradation. After 27 and 30 days, collars closed with the degradable suture material fell off of the bats. Inspection of these bats showed that the fur underneath the collars had been worn away, similar to the bald patch on a bat's back after a glued-on transmitter falls off, but there were no signs of abrasion or irritation. After 35 days, we removed the collars attached by other methods and inspected the bats' necks. The glue did not show any signs of degradation. The cotton thread had started to fray, but these collars remained securely attached up to 35 days until they were removed. Bats showed a bald area under the cotton shoelace collars, and one bat with a collar closed with cotton thread showed minor abrasion at the closure site.

The shoelace collars closed with degradable suture proved the best option that would extend attachment through 30 days (Fig. 2). We then tested this model on free-ranging *U. bilobatum* females that were tracked 4–11 h per night for 4–12 days. After collar attachment, these bats showed expected foraging and resting patterns for this species, and no visible signs of distress during visual inspection of their day roost. One female and her offspring were recaptured 15 days after initial attachment. The female was 0·5 g lighter than her original capture mass, which was less than typical daily fluctuation of body weight in this species and typical for lactating mothers who decrease in body mass until their offspring are weaned (O'Mara unpublished data), and the infant had increased mass by 1·5 g. Of the remaining three individuals, two continued to roost and forage normally for the remaining 3 weeks of collar attachment. One transmitter could no longer be located after 2 weeks, likely due to damage to the antenna of the transmitter, as the social group was still complete.

We further tested the collar design on 16 *Molossus molossus,* as this Neotropical species is particularly prone to removing devices glued to their back (mean attachment time: 3 ± 2 days), and morphological restrictions of this smaller species required small, thin collars. We tested two designs based on our previous results and collars used on closely related species (Rhodes *et al.* 2006). Collars made of 1·5-mm rubber bands or 1·5-mm nylon ribbon were attached on eight animals each and closed with degradable suture thread and a small amount of cyanoacrylate glue to ensure the knot was closed. Both collar types included dummy transmitters approximately the same size and shape as Holohil 0·3 g LB2 transmitters. *Molossus molussus* scratched at the collar with one foot, rather than pull on them like *A. jamaicensis*. Half of the bats left the collars and transmitters in place for the full time that they were in captivity (seven nights). The other half removed the collars after a maximum of two nights or repeatedly scratched the collar so that the dummy transmitter ended up under their chins. We changed the collar length of these same individuals to test whether tighter collars that stayed in place or looser collars that allowed the animal to rotate the collar around its neck were more suitable. After one night, the bats had rotated the transmitter under their necks, and only one bat spun the collar fully around to its original position. Interestingly, this appears to be individual specific, as the same individuals repeatedly removed collars, hinting at consistent personality differences within this species.

After the success with the collar design on the frugivores and poor results with *M. molossus*, the comparative study on the temperate *N. noctula* showed that this species tolerated the collars well and yielded astonishing results that significantly lengthened tracking times. In 2012, nine individuals dropped their glued transmitter after only 2 ± 2 days and seven animals migrated immediately after transmitter attachment, as they were not located during daily searches via airplane-mounted antennae and receivers. The animals in 2013 with collars were tracked 23 ± 17 days, extending tracking through transmitter battery life. One transmitter was found in a bat box during the weekly inspections 63 days after deployment. The animal was not present when the transmitter was found in the box, but the collar material looked unworn, and it had opened at the weak link as intended.

Discussion

The use of spatial tracking and telemetry is essential to understanding bat biology and behaviour. Consequently, proper device attachment is crucial for rendering such studies as successful and non-invasive as possible. Nonetheless, our literature review shows that after 50 years and almost 300 studies, there has been little or no development and even less follow-up assessment of attachment methods. The duration of attachment for transmitters glued directly to the bat, by far the most commonly used method, is short compared with what a collar-based attachment system offers. This is particularly true for animals that persistently try to remove attached devices. Other attachment methods, especially the collars used for GPS tracking, are often permanent and ethically difficult to justify given the threatened or unknown status of many species and the limited life span of devices. Furthermore, a consensus of a 'best practice' 5% relative transmitter mass and attachment, based on flying manoeuvrability measured by Aldridge & Brigham (1988), is prevalent in the literature, but we show that approximately half of the studies that use tracking do not follow this guideline and often with minimal or no justification.

From the available data, we could not quantify the effect of transmitters on bat health and survival. However, several studies indicate that if the 5% rule is followed, the effects of short-term attachment may be small or even negligible. Transmitters that weigh <5% of body mass did not appear to impact the immediate survival or behaviour of three small insectivorous bat species (Hickey 1992; Kurta & Murray 2002; Neubaum *et al.* 2005; Weinbeer, Meyer & Kalko 2006; Patriquin *et al.* 2010), particularly when compared to bats that were implanted with passive integrated transponder (PIT) tags (Neubaum *et al.* 2005). Four of 13 *M. molossus*, carrying transmitters that weighed 3·5% of body mass for up to four nights (Dechmann *et al.* 2010), were recaptured in good health 4 years later, which is the longest survival record to date for this species (Y. Gager unpublished data). This gives some indication that long-term effects on survival may be limited, at least in individual cases. The impact of these transmitters, however, may be confined to a single reproductive year rather than borne out over a longer time-scale.

In a meta-analysis of the effects of telemetry devices across bird species, transmitters of any size appear to negatively impact body condition and reproductive success (Barron, Brawn & Weatherhead 2010), and transmitter shape can significantly affect drag and flight energetics in birds (Vandenabeele *et al.* 2012). However, impact of the shape of the attached device has yet to be addressed for bats. Studies on marine mammals and fish have shown a greater effect of transmitter shape than mass (Pavlov, Wilson & Lucke 2007), and experimental work with migrating birds has also shown that minimizing drag is important to reducing the overall mechanical impact on flight (Obrecht Iii, Pennycuick & Fuller 1988). Unlike experiments with increasing body mass (Davis & Cockrum 1964; Aldridge & Brigham 1988), it is unknown how increasing drag through the shape, mass and profile of an externally attached transmitter device impacts flight energetics in bats (Norberg 1990).

In fact, we expect this effect to be at least as strong as in birds. We also expect this to correlate with wing morphology, as the relationship of wing shape to foraging strategy and ecological niche in bats is well known (Norberg & Rayner 1987). Thus, while transmitter attachment may increase overall drag (Vandenabeele *et al.* 2012), the manifestation of these effects at a physiological level within individual species may be highly variable (Gow *et al.* 2011; Elliott *et al.* 2012), and the best practice guideline of a '5% rule' for flying vertebrates across diverse morphologies and ecologies is untested (Casper 2009). It is widely accepted that narrow-winged species with heavier wing loads are more energetically limited than broad-winged species with lower wing loads (Norberg 1981; Norberg & Rayner 1987). Accordingly, relative mass should have a greater effect on the former (e.g. *M. molossus* or *N. noctula* in our study) compared with the latter (e.g. *A. jamaicensis* and *U. bilobatum*). Likewise, experiments with broad-winged, gleaning phyllostomids have shown that these species are highly manoeuvrable (Stockwell 2001) and unlikely to be encumbered by increased body mass in the same manner as a more narrow-winged, open-air flier. Broad-winged species are more flexible in their ability to manipulate wing shape (Bahlman, Swartz & Breuer 2013) to generate consistent levels of power, particularly during climbing phases of flight (Macayeal *et al.* 2011), than narrow-winged ones. Special consideration must also be taken when females are pregnant or carrying dependant offspring. Tracking studies of pregnant and lactating females are not common, often because of ethical (and legal) concerns. For those studies that have tracked pregnant females, it is not clear how the threshold weight of the transmitter was chosen. Bat foetuses are particularly heavy, especially when compared to the foetal weight of non-volant mammals [bats: 22% of maternal weight, other mammals: 8% maternal weight (Kurta & Kunz 1987)]. During late stages of pregnancy, females carry substantially heavy loads, and a simple percentage rule of their weight likely does not reflect their true load. Attachment of a device to a pregnant female compounds the burden of the transmitter, and this should ideally be minimized. The use of non-pregnant weights could be used to establish thresholds, but unless individuals are known, this would rely on species means and may not reflect individual variation. There is some indication, however, that female wing size and shape are under selection to compensate for the increased weight and transportation costs of pregnancy (Norberg & Rayner 1987; De Camargo & De Oliveira 2012), so perhaps, the addition of transmitter weight may be minor. Researchers should practice conservatism when adding any weight to their study animals. The impacts of morphology and reproductive status reinforce the need for discussion and justification for the type and weight of transmitters attached, as a single rule may not be equally applicable to all species or individuals.

Battery life of the smallest contemporary radiotransmitters is up to 21–28 days, and average tag attachment is 9 days, meaning that with the predominant currently used method, gluing, 2 weeks or more of data are potentially lost, especially in the tropics. We found only two previous studies that reported some development for device attachment (Rhodes *et al.* 2006; Smith *et al.* 2011), both of which included a collar system. In their search for the best long-term collar for large flying foxes, Smith *et al.* (2011) used several material types and shapes for the collar and device attachment and found that a simple straight collar with the antenna facing parallel to the animal's spine was the most effective.

It was our aim to find an ethically acceptable, lightweight and easy-to-copy collar design with a weak link that could be tailored to smaller species. Testing this on multiple species showed us that design suitability has to be carefully evaluated, ideally with temporarily captive animals. But where suitable (three of our four study species), these collars remove the pressure to start data collection quickly before the transmitter falls off, while allowing much longer data collection periods. It has yet to be demonstrated how long is needed for a bat to habituate to transmitter attachment, or if transmitter attachment affects behaviour in appreciable ways (increasing or delaying foraging time, decreasing social interactions, etc.). Most studies begin collecting radiotracking data the night following transmitter attachment and assume that the behaviour of the study individual has returned to normal by then. Future work comparing the first night's tracking data to subsequently sampled nights would provide a simple preliminary test of this assumption.

While we continue to refine our attachment techniques, we feel that both the use of collars to attach radiotransmitters and the captive validation of attachment are valuable in improving bat radiotelemetry. Many bat species are endangered, vulnerable or have unknown status (Racey 2009), and while tracking is essential to understanding their conservation requirements, it must be carried out in the most productive way possible. Lastly, regarding the ambiguity of the '5% rule', Amelon *et al.* (2009) proposed a 'common sense' rule used by many researchers: (i) always consider the ethics of attaching tags; (ii) consider the behaviour, load carrying capacity and wing metrics of the study animals (load carrying ability varies considerably); (iii) aim for tags that weigh <5% of the bat's body mass; and (iv) tags should definitely be <10% of body mass if carried for more than a few days until proven otherwise. To these rules, we would like to add that researchers report body masses for their study populations. With the numerous threats to bat habitats and the increasing number of cryptic species discovered, population-specific biological data are increasingly important. Additionally, future studies will need to invest more effort into building upon previous knowledge, in finding the best attachment method, size and shape for every study species to truly promote wildlife tracking while keeping to ethical standards.

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Data accessibility

Data available for download as Supporting Information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Data set collected through the literature review on device attachment.