

A PIT-tag based method for measuring individual bait uptake in small mammals

Sarah E. Beatham^{1,2}, Dominic Goodwin³, Julia Coats¹, Philip A. Stephens², Giovanna Massei¹

¹ National Wildlife Management Centre, APHA, Sand Hutton, York, YO41 1LZ, UK.

² Conservation Ecology Group, Department of Biosciences, Durham University, South Road, Durham, DH1 3LE, UK.

³ Biomotors Ltd., The Old Rectory, Boughton Malherbe, Maidstone, Kent, ME17 2BD, UK.

Corresponding author: sarah.beatham@apha.gov.uk, orcid.org/0000-0001-8300-8953

19 **Abstract**

- 20 1. Rodents and other small mammals cause an increasing number of negative economic and
21 environmental impacts worldwide. In the UK, the non-native grey squirrel has a significant impact
22 on the forestry industry and has caused the decline of the native red squirrel.
- 23 2. Baits are used to deliver biocides and contraceptives to reduce overabundant wildlife populations
24 and as vehicles for vaccines to control disease outbreaks. Bait-delivered contraceptives are also
25 being developed to manage grey squirrel populations in the UK. The effectiveness of bait-delivered
26 drugs on wildlife populations depends on the amount of bait consumed by individuals over time;
27 therefore, it is important to understand individual level bait uptake in order to optimise delivery
28 methods.
- 29 3. Passive Integrated Transponder (PIT) tags are increasingly used to mark and monitor animal
30 behaviour as they are cost-effective, have minimal negative welfare impacts and have a lower tag
31 loss rate than external tags, particularly in small animals.
- 32 4. The aim of this study was to design and test a novel bait hopper equipped with a PIT-tag reader and
33 bait weighing device, to record bait uptake by individual grey squirrels for optimising the delivery
34 of a contraceptive bait. The hopper was designed to overcome some of the limitations of traditional
35 PIT-tag systems, by improving battery life and the quality and quantity of data collected in the field.
- 36 5. In captive trials, the hopper proved to be highly effective at recording feeding visits by squirrels, as
37 95% of the visits could be attributed to a PIT-tag record. The hoppers measured the amount of bait
38 removed per feeding visit to an accuracy of 0.1 g, with 97% of the bait taken from six hoppers
39 attributed to a PIT-tag ID. In a field trial, the hoppers were effective at recording the feeding visits
40 by grey squirrels in two woods, with 47 of the 51 PIT-tagged grey squirrels entering the hoppers.
- 41 6. The adaptability of the hopper design means that it has wider applications for wildlife management;
42 in particular, efficacy studies for bait-delivered substances in the context of wildlife disease control
43 and/or population reduction.

Keywords: feeding behaviour, grey squirrel, contraceptives, biocides, microchip, *Sciurus carolinensis*, wildlife management, remote sensing.

Introduction

Rodents and other small mammals cause an increasing number of negative economic and environmental impacts worldwide, including losses to the food industry, damage to property and the transmission of diseases (Messmer, 2019). For instance, damage by rats has been estimated to cost the United States approximately \$19 billion per year (Pimentel et al., 2000). In the UK, the grey squirrel *Sciurus carolinensis* causes an estimated £10 million in tree damage per annum (Derbridge et al., 2016) and is also responsible for the decline of the native red squirrel *S. vulgaris* (Gurnell et al., 2016; Rushton et al., 2006). Baits are used to deliver biocides and contraceptives to reduce wildlife populations (Towns & Broome, 2003; Pyzyna et al., 2016) and as vehicles for vaccines to control disease outbreaks in wildlife (Slate et al., 2005). Bait-delivered contraceptives could be used to manage grey squirrel populations (Dunn et al., 2018) and this is a research objective in the current UK Government management plan for the species (Forestry Commission, 2014).

Bait markers such as tetracycline (Algeo et al., 2013), iophenoxic acid (Marks & Bloomfield, 1999) and rhodamine B (Baruzzi et al. 2017) can be used to assess bait uptake at a population level. However, the effectiveness of rodenticides, oral vaccines and bait-delivered contraceptives depends on the number of visits to bait stations by individual animals over time and the quantity of bait they consume at each visit. Consequently, understanding how bait uptake differs between the individuals in a population is important when optimising the delivery of contraceptives, vaccines and biocides.

Passive Integrated Transponder (PIT) tags are increasingly used to mark and monitor animals, as they have minimal welfare impacts, are relatively cheap and easy to apply and generally have a lower tag loss rate than external tags (Smyth & Nebel, 2013). Once a number of individuals have been PIT-tagged, Radio Frequency Identification (RFID) technology can be used to create remote sensing stations that

record and monitor the presence of individuals via their PIT-tags. PIT-tags do not rely on an internal power source, so can feasibly be used over the lifetime of an animal, providing an important improvement in animal welfare by reducing the amount of trapping and/or handling required. Examples of how this technology has been used to collect remote data on wildlife in the field include recording the behaviour of wood ducks *Aix sponsa* at nest boxes (Bridge et al., 2019), monitoring the home ranges of wood mice *Apodemus sylvaticus* using bait stations (Godsall et al., 2014) and recording den use by edible dormice *Glis glis* (Kukalová et al., 2013).

The aim of this study was to design and test a novel bait hopper, equipped with a PIT-tag reader and bait weighing device that could record the frequency of feeding visits and amount of bait consumed per visit by individual grey squirrels in a natural environment. The hopper was tested in a laboratory, in a trial using captive grey squirrels and then used to collect data on the feeding behaviour of free-living grey squirrels in two woods. The hopper was designed to overcome a number of limitations typically encountered when using RFID systems to gather long-term field data. We discuss how this hopper represents a significant improvement over other systems, in terms of data quality and quantity, battery management and practicality; in particular, we reference a bait station previously developed to record visits by PIT-tagged grey squirrels (Kenward et al., 2005). This work was carried out within the context of a larger study developing a contraceptive bait for grey squirrels and optimising its delivery in the field. We discuss how the device could be applied to studies with other small mammal species.

Materials and Methods

Technical design

The grey squirrel bait hopper was designed to record the identity of any PIT-tagged squirrel that entered it and to restrict access to bait by non-target animals through a weighted door and metal exterior (Figure 1). The positioning of the door was based on a previous hopper design developed by the Forestry

Commission to deliver the rodenticide Warfarin to grey squirrels (Mayle et al., 2007). The door pivots on a top hinge, angled to encourage a squirrel to push it open with its head in order to access the bait.

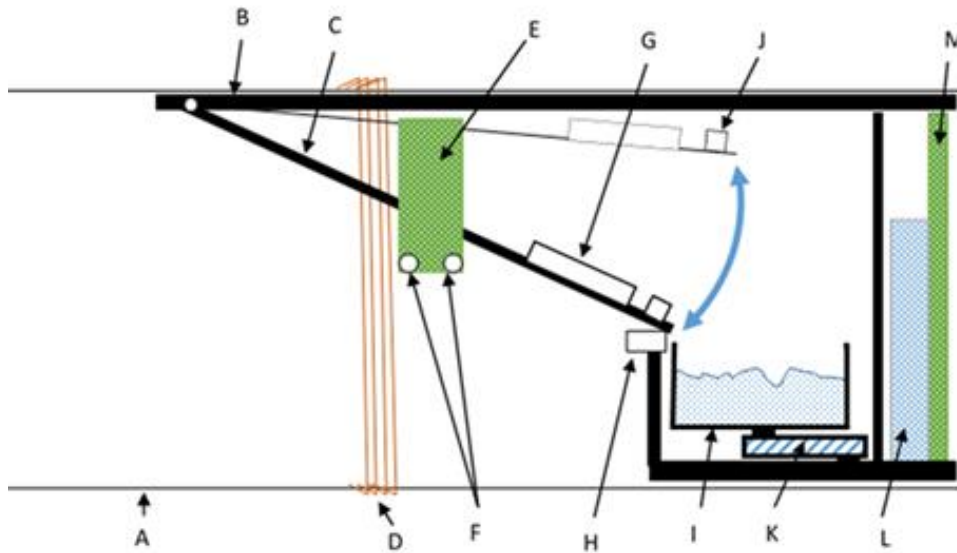


Figure 1. Design of a grey squirrel bait hopper with integrated PIT-tag reader and bait weighing capability. A. Body of hopper: a 10 x 10 x 55 cm length of aluminium tubing, entrance left. Includes a plastic section to avoid disruption of the RFID signal; B. 3D-printed plastic insert which latches into the aluminium tube; C. Pivoting plastic door; D. RFID antenna coil set to a frequency of 134 kHz; E. Light beam driver/detector circuit boards; F. Infrared light beam sensors including LED emitters on one side of the entrance and photodiode receptors on the other side, forming a dual light beam across the entrance; G. Steel weight (70 g) attached to the door flap; H. Magnet sensitive reed switch to detect when the door has been pushed open; I. Metal bait tray which can be inserted into the hopper from the side. Includes plastic runners on the base to allow secure attachment; J. Magnet attached to the door; operates the door reed switch; K. Strain gauge including grooves to attach the bait tray; L. Five AA batteries to power the data-logger; M. Main data-logger circuit board incorporating a microcontroller with non-volatile memory and clock functionality, RFID reader, LCD display, removable SD card, analogue-to-digital converter (ADC), reed switch to flush data and reed switches to set date/time.

The grey squirrel bait hopper incorporated an RFID system, produced by NatureCounters, Kent, UK. To detect a PIT-tag, an RFID system must be active, which utilises a significant amount of battery power. The system in this study conserves battery power through the use of infrared light beams. Each visit to the hopper by an animal is designated as an “event”. An event is triggered when both infrared light beams are broken, and finishes when both light beams are clear again. When an event is triggered, the RFID reader is activated, creating a frequency field in the antenna coil. The field remains active until the event has finished, a PIT-tag has been successfully read, or a timeout of approximately 3 seconds is reached. Using this system, the hopper requires only five AA batteries and can be used in the field for at least four weeks before the batteries have to be replaced.

The RFID coil in the hopper is positioned immediately before the bait compartment. This means that it is more likely that PIT-tag individual identities (IDs) will be recorded for feeding visits only, as opposed to visits where an animal partly enters the hopper and does not feed. If a PIT-tag is detected but the identification is not established, a ‘0’ is recorded. This offers an advantage over other RFID systems, which typically only record positive identities from PIT-tagged individuals.

A strain gauge, upon which the bait tray is attached, weighs the amount of bait consumed by an individual, identified by its PIT-tag record. The hopper records, via a magnetic door switch, every time the bait compartment is accessed. When combined with remote camera monitoring, this can provide valuable information on non-target animals accessing bait and an indication of the number of untagged individuals in the target population. When the door magnet is disengaged, the hopper records the weight of the bait tray at least 5 times per second, and calculates an average weight from these readings. The PIT-tag IDs, door switch and weight data associated with each event are recorded to files on the SD card, along with the date and time.

Captive trial to test hopper capacity to record feeding visits by squirrels

The trial was conducted using two outdoor pens (width = 2.7 metres, length = 9.7 metres, height = 2.4 metres), each containing one male and two female grey squirrels previously fitted with a PIT-tag (Identichip®, York, UK) subcutaneously in the scruff of the neck. Throughout the trial, the squirrels

were provided with a varied diet including maize, peanuts, bird seed and fruit, along with environmental enrichment including wool bedding, foliage, tubes, ropes, nest boxes, branches and sticks. Two hoppers were placed in each pen and each hopper was positioned on top of a wooden stand (approximately 90 cm high) so that they were visible by closed circuit television (CCTV) cameras. During the trial, one of the hoppers became obscured by a branch so was not included in the study. For four consecutive days per week, for two weeks, 10 g of fresh hazelnut paste was provided daily in each hopper. Feeding visits to the hoppers by individual squirrels were recorded using CCTV at peak times of feeding activity (4:00 to 8:00 and 16:00 to 20:00) in the second week of the trial. For the CCTV analysis, when a squirrel entered a hopper, the visit was assigned to one of the following categories: ‘feeding’ (when it entered the hopper and was subsequently observed masticating), ‘full’ (only the tail was visible and no evidence of feeding) or ‘partial’ (part of its hind quarters were still visible). Only visits that could be definitively assigned to one of these categories were used in the analysis.

The accuracy with which the hoppers recorded feeding visits was determined by checking whether a PIT-tag was detected for each feeding, full or partial visit recorded on CCTV and whether the ID of the squirrel was established. A Fisher’s exact test was used to determine whether PIT-tag IDs were more likely to be recorded for feeding visits over non-feeding visits.

Field trial to test hopper capacity to record feeding visits by squirrels

A field trial was conducted in December 2018 in two 8 ha woods located in Yorkshire, UK. Single-catch squirrel cage traps (n=24) were deployed in each wood on one metre high wooden stands and pre-baited with peanuts and whole hazelnuts every two to three days for one week. Grey squirrels were trapped the following week over consecutive days. Traps were set early in the morning and checked in the afternoon. Trapped squirrels were anaesthetised using isoflurane via a mask, sexed and a PIT-tag (Identichip®, York, UK) implanted subcutaneously in the scruff of the neck. Hair was clipped from the end of the tail for visual identification. Once recovered from anaesthesia, squirrels were released under a Natural England licence in the location at which they had been trapped.

Trapping was continued until it was estimated that the majority of the population had been PIT-tagged, based on the ratio of new individuals to recaptured (tail clipped) individuals per day. In both woods, within three weeks of PIT-tagging, each trap was replaced by a hopper, fixed to the wooden stand. To simulate the deployment of a contraceptive bait, each hopper was pre-baited with 40 g of hazelnut paste every two to three days for one week. The following week, each hopper was baited daily with 40 g of hazelnut paste for four consecutive trial days. The trials for both woods were conducted consecutively, using the same hoppers.

All analyses were carried out in R (R Core Team, 2019) using the MASS package (Venables & Ripley, 2002). A linear model (assuming a Gaussian distribution) was used to test whether there was a significant relationship between the number of feeding visits (or PIT-tag records) per individual and the sex of individuals or the wood where they were trapped. Significance was tested using type II analysis of variance. A generalised linear model (GLM, assuming a negative binomial distribution) was used to test whether there was a significant relationship between the number of hoppers visited per individual and the sex of individuals or the wood where they were trapped. Significance was tested using type II analysis of variance with a likelihood ratio test (LRT). Diagnostic checks of residual plots for both models showed that the residuals were approximately normally distributed and model assumptions were met.

Laboratory trial and captive trial to test hopper capacity to measure bait uptake by individual squirrels

A trial was designed to test the accuracy of the built-in weighing scales in each hopper, using manually weighed baits. To measure the accuracy of bait weight taken per visit, the first part of the trial was conducted in a laboratory with nine hoppers. Approximately 70 g of 100% hazelnut paste was weighed in a bait tray and placed in each hopper. To simulate different field conditions, five hoppers were placed in a refrigerator and left for one hour to acclimatise to between 6°C and 8°C; the remaining four hoppers were left at room temperature, between 20°C and 21°C. A small amount (0.1 to 2.2 g) of paste was then removed from each hopper using a pre-weighed metal spoon, and the spoon and paste weighed (to the

nearest 0.1 g). After at least 10 minutes, a larger amount of paste (4.9 to 18.5 g) was removed from each hopper and weighed (to the nearest 0.1 g). This was repeated until there were at least 5 weights for small amounts of bait and at least 5 weights for larger amounts of bait for each hopper. To ensure the strain gauge was stable, the amount of bait taken from each hopper was calculated from the weight recorded by each hopper 2 minutes prior to the bait removal minus the weight taken 2 minutes after the removal. These were compared with weights obtained manually using a standard balance.

To test whether it was possible for the hoppers to weigh bait consumed by individual squirrels, a second trial was conducted using captive PIT-tagged grey squirrels. Two hoppers per pen were deployed in three outdoor pens containing 2-3 squirrels per pen, 7 squirrels in total. Hoppers were placed on the floor along each side of a pen, weighed down by bricks, to ensure the squirrels could not move or overturn them. In week 1, the hoppers were baited on Monday, Wednesday and Friday with approximately 40 g 100% hazelnut paste to encourage the squirrels to use the hoppers. On the Tuesday and Wednesday of week 2, 20 ± 0.5 g of hazelnut paste was weighed into bait trays and installed in each hopper at 7:15 am, immediately before the squirrel peak feeding time. After 6 hours, the bait trays were removed and the remaining bait weighed (to the nearest 0.1 g). The manual weights taken for each trial period were compared to those recorded by the hoppers. The weight of bait taken for each event was calculated by taking the minimum weight from the most stable values recorded; those where there was less than 5 units difference between the first and fifth repeat reading. The weight decrease at each event was then matched with a PIT-tag record, if available, to calculate the amount of bait taken per visit by individual squirrels.

Results

Captive trial to test hopper capacity to record feeding visits by squirrels

In total, 97 feeding visits, 47 full visits and 102 partial visits to the three hoppers by grey squirrels were recorded on CCTV during the trial. Feeding visits were recorded for five of the six squirrels and full

and partial visits for all six squirrels. An average of 27 (range = 9 to 48) PIT-tag records were obtained for each squirrel. A PIT-tag was detected for 100% of feeding visits, 96% of full visits and 64% of partial visits; a PIT-tag ID was established for 95% of feeding visits, 77% of full visits and 25% of partial visits. The percentage of PIT-tag IDs recorded was significantly higher for visits where bait was taken (95%), compared with visits where no bait was taken (41%, $p < 0.001$). The ratio of feeding visits recorded by CCTV to PIT-tag IDs was 1:1.6, as the hoppers would sometimes record multiple IDs for an animal that spent more time inside them. On 28 occasions, it was observed that the squirrel visiting a hopper was displaced by another squirrel.

Field trial to test hopper capacity to record feeding visits by squirrels

In wood 1, on three trap days, 21 adult squirrels (13 females and 8 males) were trapped, PIT-tagged and released; the percentage of the total number of squirrels PIT-tagged each day was 86%, 14% and 0%. In wood 2, on four trap days, 30 adult squirrels (16 females and 14 males) were trapped, PIT-tagged and released; the percentage of the total number of squirrels PIT-tagged for each trap day was 40%, 40%, 10% and 10%.

In wood 1, on the four trial days 24 hoppers logged 1,582 PIT-tag records and each hopper recorded visits from 2 to 8 squirrels, with 17 hoppers visited by least 4 individuals. In wood 2, on the four trial days, 24 hoppers logged 2,844 PIT-tag records and each hopper recorded visits from 1 to 8 squirrels, with 19 hoppers recording visits from at least 4 individuals.

Overall, 19 of the 21 (90.5%) PIT-tagged squirrels in wood 1 visited at least one hopper, all within the first 24 hours of pre-bait and 18 squirrels visited during the four trial days. In wood 2, 28 of the 30 (93%) PIT-tagged squirrels entered hoppers, all within the first 72 hours of prebait and 26 squirrels visited during the four trial days. The number of PIT-tag records per squirrel did not differ significantly between woods ($F=0.96$, $df=1$, 50, $p=0.33$); however, on average, more PIT-tag records were recorded for males than females ($F=4.6$, $df=1$, 50, $p=0.04$; Fig. 2 a). The median number of PIT-tag records was 77 for females and 107 for males.

The number of hoppers visited by individual PIT-tagged squirrels did not differ significantly between woods (LRT= 1.51, df=1, p=0.22); however, males visited a higher number of hoppers than females (LRT=5.56, df=1, p=0.02; Fig. 2 b). The median number of hoppers visited was 4 for females and 6 for males.

During the field study, temperatures ranged from -4 °C to 14 °C. Low temperatures did not affect hopper function and no hopper faults were recorded for wood 1. In wood 2, 3 of the 24 hoppers deployed stopped recording PIT-tags on the final two trial days, due to a migration in the RFID frequency range, likely caused by wet weather conditions affecting the electronics. Each hopper functioned throughout the two trials conducted over four weeks on the same set of batteries.

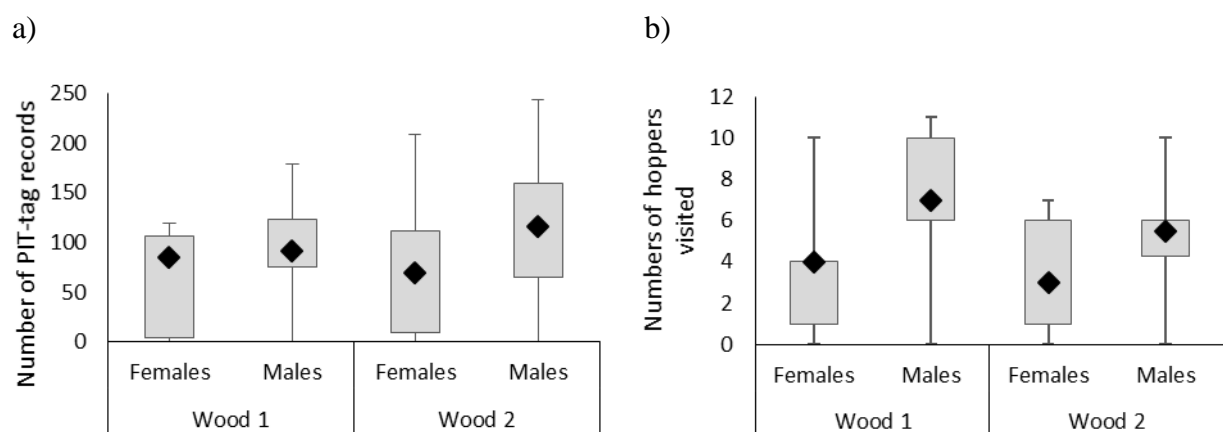


Figure 2. The number of PIT-tag records (a) and the number of hoppers visited (b) logged for 22 male and 29 female PIT-tagged grey squirrels in two woods during 4 consecutive trial days. Median values are shown by diamonds, 50% of the records for each group are shown by boxes and minimum and maximum values are shown by whiskers.

Laboratory trial and captive squirrel trial to test hopper capacity to measure bait uptake by individual squirrels

Over 90 occasions of bait removal, the average difference between the manually weighed bait removed and the weights recorded by the hoppers was 0.3 g (range = 0.0 to 5.6). The seven highest differences (all greater than 1 g) were recorded by one hopper. When the data from this hopper were removed from the analysis, the average weight difference was 0.1 g (range = 0.0 to 0.9).

The average amount of bait taken by squirrels during the captive trial was 11.5 g (range = 0.0 to 23.5) per hopper per day. The average difference between the manually weighed bait weights and the weights recorded by the six hoppers on both trial days was 0.5 g (range = 0.1 to 1.2). All seven PIT-tagged squirrels were recorded feeding from the hoppers. In total, on the two trial days, 138 g of bait was removed from the six hoppers. All of the bait consumed could be attributed to an unconfirmed PIT-tag, while 122 g could be attributed to a positive PIT-tag ID. On trial day 2, 12 g were removed from one hopper that later stopped recording PIT-tag IDs, with the fault likely caused by wet weather conditions. The average amount of bait taken by a squirrel on each visit was 1.2 g (range = -0.4 to 6.9). On one occasion there was a mis-read PIT-tag but the error concerned the last two digits of the thirteen digit ID only and was easily corrected.

Discussion

The squirrel hopper with integrated PIT-tag reader proved effective for measuring patterns and quantities of bait uptake by individual grey squirrels and the results in this study represent a significant advancement when measuring the dose rates of rodenticides, oral vaccines and contraceptives and other bait-delivered drugs. A PIT-tag was detected for every feeding visit made to a hopper by a grey squirrel in captivity, a PIT-tag ID was recorded for 95% of individuals that fed from a hopper and 97% of the bait taken from functioning hoppers could be attributed to a PIT-tag ID. A PIT-tag ID was more likely to be recorded for visits where bait was taken than those where it was not. In other bait station designs, the RFID reader has been positioned at the entrance of the feeder, rather than immediately before the bait compartment (Kenward et al., 2005). This will increase the likelihood that PIT-tags will be recorded for squirrels who visit or pass the feeder but do not take any bait.

A novel component of the hopper design was the addition of a strain gauge to weigh the bait taken on each visit. When combined with the PIT-tag data using numbered events, the amount of bait taken on each visit by individual squirrels was measured to an accuracy of 0.1 g. Remote devices with strain gauges have been used to measure the body weights of animals (Bosch et al., 2015) but none have demonstrated the accuracy of weighing necessary to calculate the dose rates of contraceptives or other drugs.

The hoppers proved to be highly effective at delivering bait to grey squirrels in two woods, with the squirrels showing little neophobia towards these devices. This can be partly attributed to the design of the door used to access the bait. Other studies have found some types of door designs can deter squirrels through the way they move or the noise that they make (Kenward et al., 2005). Overall, 47 of the 51 squirrels PIT-tagged were subsequently recorded by the hoppers within 72 hours of bait deployment. It is unknown whether the remaining four individuals had lost their tags, left the study area before the trial or whether they were present but would not enter the hoppers. Low rates of tag loss and mortality have been found when PIT-tagging bats (van Harten et al., 2019) and ground squirrels (Schooley et al., 1993) and this study provides further evidence that PIT-tagging is a reliable method for gathering behavioural data on small mammals in their natural environment.

For maximum efficacy, oral contraceptives should primarily target the females in a population (Massei & Cowan, 2014). The PIT-tag data gathered in the field in this study showed large variations in the numbers of visits to hoppers by individual squirrels and, on average, males visited more hoppers and made more feeding visits than females. These data indicate that some social factors, such as dominance, may influence feeding behaviour in grey squirrel populations. This is supported by the findings of other studies (Lawton et al., 2016) and in this study the displacement of squirrels from hoppers by other squirrels was observed. However, most hoppers were used by multiple individuals and the majority of females fed multiple times and from more than one hopper. These results suggest that social factors should not significantly reduce bait delivery effectiveness, providing the ratio of hoppers to squirrels is adequate.

Research requiring marked individuals has traditionally relied on external tags, which have the potential to be lost, damaged or mis-read, and often require some kind of human intervention, through recapture or tracking, to gather data (Gibbons & Andrews, 2004). This study further demonstrated that the detection of PIT-tags using hopsers can be achieved remotely, with minimal human interference and a high identification accuracy. This method therefore represents an improvement in welfare standards and behavioural data quality for animal research and provides a practical and accurate method to determine individual bait uptake in field conditions where otherwise multiple captures of animals would be required.

The hopsers were relatively robust, with few failures, despite wet and cold weather conditions during the trials. The few hopper faults that were recorded were likely caused by wet conditions affecting the electrical circuits and can be easily mitigated against with improved weather-proofing. The battery management system meant there were no issues with battery life during the captive or field trials, with each hopper functioning for four weeks on the same set of five AA batteries. Other studies have not been able to demonstrate the same degree of longevity, despite using larger batteries such as car batteries to power bait stations (Kenward et al., 2005). Larger batteries reduce the portability and practicality of devices for use in the field and the regular monitoring and changing of batteries can be labour-intensive and could potentially disrupt the focal species' natural behaviour. Alternatively, to reduce power consumption, RFID systems can be programmed to activate at intervals when PIT-tagged individuals are more likely to be present (Bridge et al., 2019), but this will often result in some loss of data and is unsuitable if 24 hour monitoring is required.

The 3D-printed insert upon which the electronics are fixed allows the hopsers to be easily modified; therefore, the hopsers can be adapted to record other types of data from different animal species. Adaptations of the RFID system described in this study are currently being used in studies on other small mammals (NatureCounters, 2020) including the monitoring of burrow use by European hamsters and a weighing device for measuring the body weights of a captive colony of fruit bats. By assessing patterns of bait consumption in representative population samples, adapted hopsers could be used to model the efficacy of bait delivery campaigns and inform bait delivery strategies at a larger scale. This

could include vaccines to control wildlife disease such as an oral rabies vaccine for the Small Indian Mongoose *Herpestes auropunctatus* (Vos et al., 2013) or oral contraceptives for the control of other overabundant wildlife, such as the Norway rat *Rattus norvegicus* (Pyzyna et al., 2016).

Conclusion

The novel design of hopper with integrated PIT-tag reader and bait weighing capability proved highly effective at measuring patterns and quantities of bait uptake by individual grey squirrels. The unique modifications to the hopper design in this study resulted in improved data collection and battery life in the field when compared to other similar devices. The adaptability of the hopper design means that it has wider applications for wildlife management; in particular, efficacy studies for bait-delivered drugs in the context of wildlife disease control and/or population reduction.

Ethical statement

This study was approved by APHA's Animal Welfare and Ethical Review Body (AWERB) and regulated under the Animal Scientific Procedures Act (1986).

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Author's contributions

Sarah Beatham, Giovanna Massei, Philip Stephens and Dominic Goodwin conceived the ideas and designed methodology; Sarah Beatham and Julia Coats collected the data; Sarah Beatham analysed

the data; Sarah Beatham led the writing of the manuscript with input from Dominic Goodwin, Giovanna Massei and Philip Stephens. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data available from the Dryad Digital Repository doi:10.5061/dryad.jq2bvq888 (Beatham, 2021).

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